THE WOLVERINE IN BRITISH COLUMBIA:
DISTRIBUTION, METHODS OF DETERMINING AGE
AND STATUS OF GULO GULO VANCOUVERENSIS

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

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THE WOLVERINE IN BRITISH COLUMBIA: DISTRIBUTION, METHODS OF DETERMINING AGE AND STATUS OF *GULO GULO VANCOUVERENSIS*

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Abstract

A systematic study of wolverine was carried out using cranial measurements from samples collected from the British Columbia mainland, Vancouver Island and Yukon Territory. Distribution of wolverine was established from trapping locations of specimens and sighting reports. Interviews with people on Vancouver Island aided in determining distribution for the Island.

Correlations between cranial parameters and absolute and relative age were used to examine the effect of age on skull dimensions. A non-parametric test, Kendall's tau, was used for the former and a one-way analysis of variance (Scheffe's test) for the latter. No significant correlations between cranial dimensions and absolute age were evident, hence division according to age was unnecessary. For age class comparisons, several measurements distinguished juveniles from adults in pooled samples although variability was high. The value of a relatively new aging method, the enamel-line technique, was examined. Juveniles were distinguished from adults in pooled samples but the method is not recommended for aging wolverine due to high variability and difficulty in application. The value of cementum analysis for aging wolverine is discussed.

Inter-sex and inter-regional comparisons were carried out using a multivariate technique, discriminant analysis. Correct classification of 85.7%, 100% and 100% was achieved for mainland, Island and Yukon sexes, respectively. 94.1%, 100% and 42.9% of males, and 87.5%, 100% and 85.7% of females were correctly classified for mainland, Island and Yukon regions, respectively. Both inter-sex and inter-regional differences are not consistent and cannot be applied to the species as a whole. Differences between regions are not as great as for sexes. Males display greater variability than do females. The mainland sample displays the greatest variation among the three, indicating there may be more than one regional population on the mainland. Inter-regional differences are slight and interpreted as a result of environmental modifications. Results do not support subspecific classification for Gulo gulo vancouverensis.

Wolverine in British Columbia are of general distribution. Wolverine on Vancouver Island are rare and occur mainly in the central mountainous regions. Habitat requirements and population characteristics need to be determined for Gulo in British Columbia.

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1 INTRODUCTION

There is some confusion as to the correct scientific name for wolverine. Hall and Kelson (1959) recognize four subspecies, Gulo luscus katschemakensis (Kenai Peninsula, Alaska), Gulo luscus luscus (continental North America), Gulo luscus luteus (California) and Gulo luscus vancouverensis (Vancouver Island). Banfield (1974) refers to Canadian wolverine as Gulo gulo luscus and Gulo gulo vancouverensis . Krott (1960), Rausch (1953) and Corbet (1966) recommend Eurasian wolverine (Gulo gulo) be considered synonomous with Gulo luscus in North America, the former name having priority. This report refers to North American wolverine as Gulo gulo and the Vancouver Island subspecies as Gulo gulo vancouverensis.

The wolverine is one of the least known of large carnivores in North America. Its biology and ecology has been well studied in Europe, by Krott (1959), Haglund (1966), Pulliainen (1968) and others. Recently there has been an upsurge of interest in the wolverine. Liskop et al. (1980) inspected uteri from carcasses taken in northwestern British Columbia from 1976 to 1979 and reported on aspects of wolverine reproduction. Hornocker and Hash (1981) studied a free ranging population in Montana by using radio telemetry and track counts. Magoun (Anonymous, 1980, 1981) is currently investigating the ecology of a wolverine population in Alaska.

Earlier studies are few. Wright and Rausch (1955) and Rausch and Pearson (1972) reported on reproduction of the wolverine in Alaska and the Yukon and commented on age determination. Flook and Rimmer (1965) noted cannibalism in starving wolverines and suggested a method of identifying sex from skull fragments. Newby and Wright (1955) commented on distribution of wolverine in Montana.

The focus of this study is on wolverine in British Columbia, particularly the status of the Vancouver Island wolverine, Gulo gulo vancouverensis. Goldman (1935) described this subspecies on the basis of only the type specimen and one other skull. Cowan (1936) examined two additional skulls and failed to substantiate the differences found by Goldman. He concluded that the subspecies is at best a feebly characterized race but that the designation may be corroborated by additional external characteristics (Cowan, 1936). G. g. vancouverensis is rarely seen and has not been subject to study. van Zyll de Jong (1975) noted that no additional information was available on the

subspecies.

This report re-evaluates the status of the Vancouver Island wolverine and reports on age determination in Gulo, particularly the evaluation of a relatively recent method, the enamel-line technique.

1.1 Objectives

My objectives are:

1. to re-evaluate the systematic status of Gulo Gulo vancouverensis by comparing specimens of wolverine taken on Vancouver Island and the mainland, and to determine whether the designation of subspecies is warranted. A sample of Yukon skulls is used as a reference to compare magnitude of differences.

2. to determine distribution and abundance of wolverine on the mainland and on Vancouver Island.

3. to determine if age of wolverines can be estimated by

   a. simple non-destructive measurements

   b. from cranial dimensions.

My objectives will be met by testing the following hypotheses:

H1: Skull measurements of wolverine taken on Vancouver Island differ significantly from wolverine obtained on the mainland.

H2: Length of the canine teeth is negatively correlated with age.

H3: Distance from the alveolus to the enamel line of the canine is positively correlated with age (enamel-line technique).

H4: Certain cranial dimensions are correlated with age.

1.2 Biogeography and Glaciation

Insular populations are clear examples of the process of evolution; isolation being one of the key factors which permits evolutionary change (Dobzhansky, 1951). In a freely inbreeding population there is an even distribution of genetic variability and speciation is unlikely. Once a small part of that population becomes isolated however, such as on an island, any variability that might arise is confined to that population. A smaller population is also unlikely to possess the same genetic composition as the parent population (Mayr, 1969). Since the time of Darwin and Wallace, many have realized the potential of islands for evolutionary studies (a few being Marshall, 1940; McCabe and Cowan, 1945; Dobzhansky, 1957; Anderson, 1960; Foster, 1965).

Vancouver Island is the largest of North America's offshore islands with an area of 32,100 km^2. Many land mammals are endemic to the island including white-footed mice (Peromyscus maniculatus angustus, P. m. interdictus), cougar (Felis concolor vancouverensis), raccoon (Procyon lotor vancouverensis), wandering shrew (Sorex vagrans isolatus), black bear (Ursus americanus vancouveri), Roosevelt elk (Cervus elaphus roosevelti), wolf (Canis lupus crassodon), mink (Mustela vision evagor), and marmot (Marmota vancouverensis) (Cowan and Guiguet, 1965).

The Pleistocene epoch marks the time of the most recent ice age in Canada. The chronology of the advance and retreat of glaciers is still uncertain and largely based on estimates. Flint (1947) notes that all we can confidently say is that the last major glaciation occurred within the last 30,000 years and the Pleistocene as a whole spanned at least 300,000 years, perhaps much more. There are believed to have been four major advances of ice in eastern North America and at least two in the west (Foster, 1965). The last in the west, the Vashon (last stage of the Fraser glaciation) corresponds with the final in the east, the Wisconsin, and is believed to have lasted 100,000 years (Foster, 1965).

The wolverine is thought to have evolved in the Old World and emigrated to North America from Asia across the Bering Strait during the second last glaciation (mid Pleistocene) and consequently is a relative newcomer (Kurten and Rausch, 1959; Kurten 1968; Irving, 1972). The species' original distribution in North America remains unknown; currently it is holoarctic,

occurring in northern Europe, Asia and North America.

Harington (1975) suggests that the evidence of species such as musk ox, mastodon, mammoths, horse and Bison sp. on Vancouver Island during the late Pleistocene indicate that land connections existed with the mainland. He believes these connections occurred twice during the last glaciation and at least once during the previous Illinoian glaciation. The most recent connection probably existed just prior to the time of maximum development of continuous ice, during the Fraser glaciation about 20,000 years ago (Heard, 1977). At this time sea level was depressed about 120 meters below present levels and a narrow corridor would have joined Port Angeles and Victoria (Heard, 1977). During the peak of the Illinoian glaciation (about 100,000 years ago) sea levels are estimated to have been 160 meters below present levels and an even wider corridor would have joined Vancouver Island with the mainland (Heard, 1977).

It is doubtful wolverine utilized these land bridges to cross to Vancouver Island as conditions on the island were unsuitable for its survival. Heard (1977) and Heusser (1960) provide geological and paleontological evidence which indicates that both nunataks and coastal refugia existed during the Vashon glaciation, which covered most of Vancouver Island. The survival of two well differentiated species, the Vancouver Island marmot, Marmota vancouverensis (Heard, 1977) and a ptarmigan species, Lagopus leucurus (McCabe and Cowan, 1945) is suggested on these nunataks and refugia. However, these alpine refugia would be insufficient to support a large carnivore such as the wolverine.

The marmot is the only Vancouver Island land mammal which has diverged to the point of being called a separate species. The absence of striking differentiating characters in G. g. vancouverensis probably indicates a relatively recent migration to the Island. Foster (1965) notes that it is not possible to equate degree of morphological divergence with length of time of isolation as there is too much variation between groups. Conversely, Podloucky (1977) concluded that there was a correlation between the degree of interpopulation differences in the Norway rat, Rattus norvegicus, and length of isolation. Degree of isolation is an important contributor to the extent of divergence but the amount of variability within the species in question must also be considered.

Zeuner (1950) and Rensch (1959) believe the average age of a species to be between 100,000 and 1 million years, and of a subspecies, 10,000 to 100,000 years. However, genetic changes

have been shown to arise in very short periods. Marshall (1940) considers the endemic races of small mammals on the Salt Lake Islands to have evolved in less than 20,000 years while Durrant (1952) places some of the same races at only 2,000 years. A cottid fish became distinct after less than 8,500 years of isolation (Lonnberg, 1929) and the seal Phoca vitulina is believed to have differentiated in 3,000 to 8,000 years (Doutt, 1942). Factors affecting the rate of evolution include the degree of isolation, the force of selection, the size and stability of the population and the "founder" principle (Foster, 1965; Cox and Moore, 1980). Depending on the above factors a species or subspecies may arise much earlier than indicated by Zeuner (1950) and Rensch (1959).

1.3 The "subspecies"

There has been much controversy surrounding the usage of the term "subspecies" (Wilson and Brown, 1953; Mayr, 1963, 1969; Bunnell and Williams, 1980). Before one can even start to consider whether the Vancouver Island wolverine is a subspecies, the term must be clearly defined.

No non-arbritrary criterion is presently available to delimit the category. Mayr (1964) defined the subspecies as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species and differing taxonomically from other populations of the species". Bunnell and Williams (1980) define subspecies as populations that differ recognizably from each other but can interbreed; interbreeding occurs sufficiently rarely so that genetic integrity is maintained.

Everyone seems to have their own pet definition. Edwards (1954) recognized six types of subspecies, based on the type of isolating barrier. He defined subspecies as "natural, obviously different populations, the members of which would crossbreed rather freely if they occurred sympatrically and synchronically under natural conditions but which are distinctly separated during their mating period" (Edwards, 1954). Here lies the problem, what is meant by "obviously different"?

This lack of an exact definition has been cited as evidence by those that wish the term abolished. It has been called inconvenient, misleading and said to lack value as a discrete

taxonomic unit (Bunnell and Williams, 1980). Wilson and Brown (1953) recommended doing away with subspecies, citing four aspects they felt severely reduced the term's usefulness:

1. the tendency of different characters to show independent trends of geographic variation.

2. the independent reoccurrence of similar or phenotypically indistinguishable populations in geographically separated areas (polytopic species).

3. the occurrence of microgeographic races within a formally recognized subspecies.

4. the arbitrariness of the degree of distinction considered by different specialists as justifying subspecific separation of slightly differentiated local populations.

Inger (1958) argues that Wilson and Brown (1953) magnify exceptional cases and do not provide sufficient evidence to obliterate a useful concept. Controversy has arisen due to the wide misuse of the term. It has been applied to physiological variations, genetic minorities, micropopulations, seasonal generations, geographical populations, aberrations, and almost any other kind of infraspecific grouping (Fox, 1955). Inger (1958), Mayr (1969) and Bunnell and Williams (1980) do not consider the subspecies an evolutionary unit. A dynamic and continuous pattern cannot be partitioned into artificially created discrete units (Bunnell and Williams, 1980). "Species are not composites of uniform subtypes, subspecies, but consist of an almost infinite number of local populations, each in turn consisting of genetically different individuals." (Mayr, 1963). The better geographic variation of a species is known, the more difficult it is to delimit the subspecies; many such delimitations being quite arbritrary (Mayr, 1973).

This is not to say that the subspecies has no value. The naming of the term is unfortunate and carries evolutionary connotations which do not apply. I agree with Bunnell and Williams (1980) who define the subspecies as a category of convenience used when our understanding of variability will be increased by establishing discrete geographically bounded units within a potentially interbreeding population or species. Using

properly defined criteria it is a valuable classification tool and is highly legitimate (Fox, 1955; Durrant, 1955; Bunnell and Williams, 1980). The subspecies concept has recently become important in mustelid management as one objective of the Fish and Wildlife Branch is to maintain the diversity of species representative of the major biophysical zones of the province (Fish and Wildlife Branch, 1979).

The term subspecies in this report is used strictly as a category of convenience, with the primary aim of delimiting morphological variation.

1.4 Age Determination

Age determination is essential in systematic studies. Without accurate aging techniques one cannot assess the uniformity of material to be compared and the nature of age dependent variability (Klevezal and Kleinenberg, 1967). Information about the age of mammals is also necessary to understand many aspects of their biology and is a vital part of conservation and wildlife management. A thorough analysis of the population dynamics of a wildlife species (eg., growth rate, time of sexual maturity, timing of reproductive cycles, longevity, etc.) is impossible without reliable age estimates (Klevezal and Kleinenberg, 1967; Morris, 1972).

Age determination in wolverine has not been extensively researched. This study evaluates the use of simple non-destructive techniques that may be used in the field. Not only would this have important implications in wolverine biology but may be applicable to other mammals. Aging wolverines by certain cranial dimensions is also examined.

2 MATERIALS

Skull specimens originated from three localities, Vancouver Island ("Island"), the British Columbia mainland ("Mainland") and the Yukon Territory ("Yukon"). Sample sizes used in this study were 8 Island (4 male, 2 female, 2 unknown), 58 Mainland (30 male, 19 female, 9 unknown), and 14 Yukon (7 male, 5 female, 2 unknown). Measurements were either taken on the premises where specimens were held or skulls were borrowed.

Vancouver Island skulls are held at the British Columbia Provincial Museum (BCPM), (n=4); Cowan Vertebrate Museum, University of British Columbia (UBC), (n=2);, the United States National Museum (USNM), (n=1); and the private collection of Bud Frost, Port Alberni, B.C., (n=1). The USNM skull was measured by museum personnel and not seen. Vancouver Island skulls are listed in Table 1.

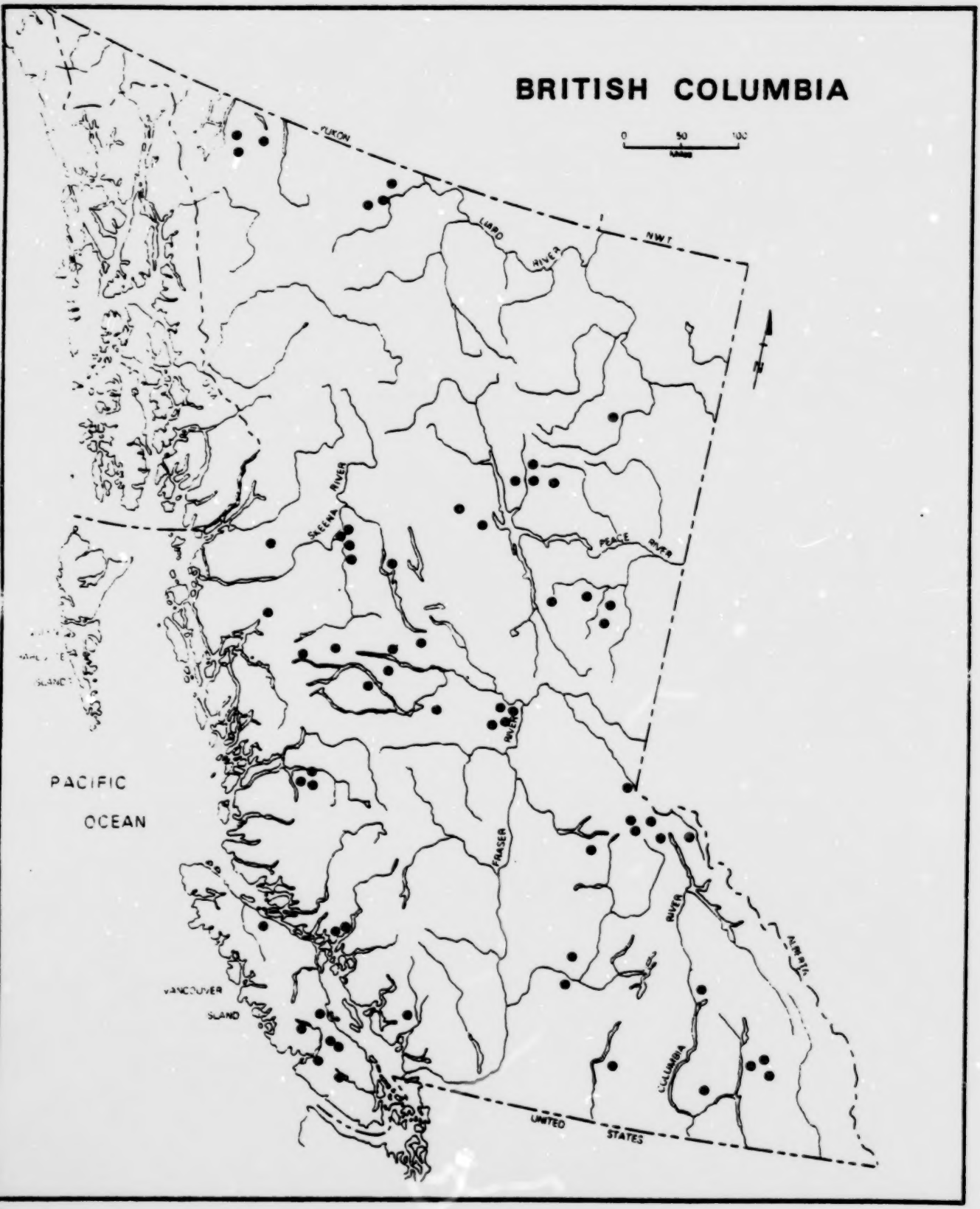
Mainland specimens are held at the BCPM and at UBC (Appendix 1). The series of aged skulls used in my analyses (12 females and 22 males) was part of a donation to the BCPM by Karen Liskop of Simon Fraser University, Burnaby, B.C. This series was collected in a reproductive study by Liskop et al. (1980) which utilized carcasses obtained from trappers in northwestern British Columbia from 1976 - 1979. A commercial histologist, Matson's, of Montana, aged the lower left canines by cementum analysis (Liskop et. al., 1980). Thirteen Yukon skulls were borrowed from the Yukon Department of Renewable Resources, Whitehorse. One Yukon specimen was located at UBC.

Skulls were grouped according to sex and geographical origin. The distribution of specimens used in the analyses as determined by trapping locations is shown in Figures 1 and 2.

The 3 Vancouver Island and 4 mainland (1 Washington) pelts held by the BCPM were examined and photographed.

Table 1. Vancouver Island specimens (Sex for unknowns is as determined by discriminant analysis and age class is as reported. A=adult U=unknown)

I.D.#	Date	Sex	Age	Location
UBC 1745	Jan. 17, 1946	F	U	Tsable River
UBC 3510	Feb., 1949	U(M)	U	Cameron River
BCPM 1343	May, 1891	M	U	unknown
BCPM 1570	winter, 1907	M	U	Cowichan Lake
BCPM 2486	Nov., 1937	M	U	Cameron River
BCPM 9872	July 31, 1978	F	A	Rooney Lake
USNM 211499	Mar. 27, 1913	M	A	Great Central Lake
Frost	1920's	U(F)	U	Coleman Creek



igure 1. Map showing locations of specimens for Mainland and Island samples from trapping locations (1 Island skull not indicated as location unknown).

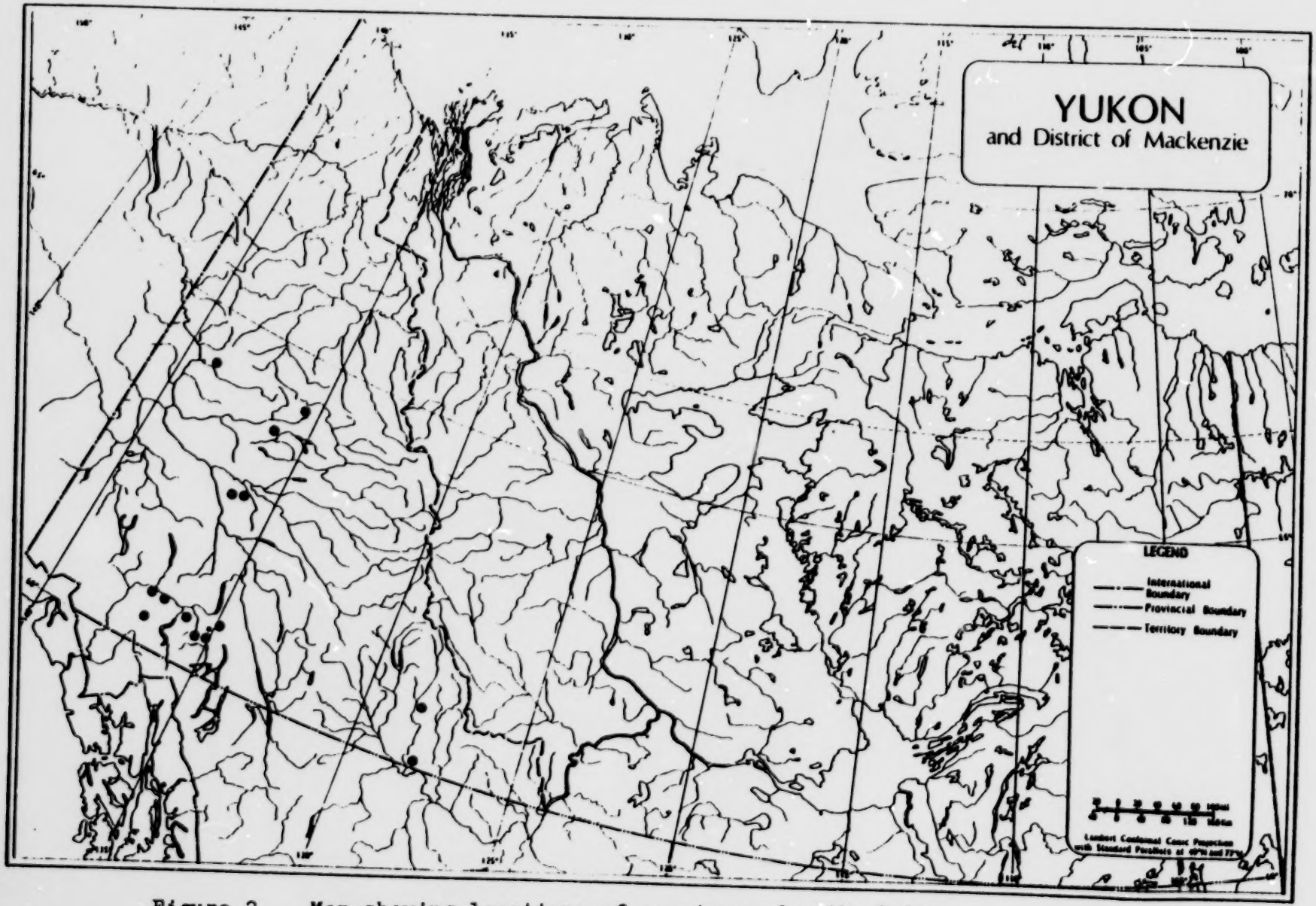


Figure 2. Map showing locations of specimens for the Yukon sample from trapping locations.

3 METHODS

3.1 Distribution

A distribution map of Gulo gulo on the British Columbia mainland was compiled from sighting reports in the literature, BCPM sighting records, data from Holbrow (1976) and trapping locations. The latter are those of specimens held by the BCPM, UBC and those of carcasses used by Liskop et al. (1980) and contained in BCPM records (a listing of all specimens according to management unit is found in Appendix 3). Distribution of G. g. vancouverensis was determined from locations where specimens were trapped, sighting reports in the literature and those held by the BCPM, unpublished sightings and interviews with biologists, conservation officers and trappers on Vancouver Island.

3.2 Measurements

Nineteen cranial and 8 canine dimensions were measured with a vernier caliper to the nearest 0.1 mm (Figures 3 and 4, Tables 2 and 3). Several ratios involving condylobasal length were also computed. The right canine and right side of the skull were used except in cases of damage when the left side was used. For enamel line distance I averaged the left and right measurements for upper and lower canines. Length of saggital crest extension was indirectly derived from length of skull minus condylobasal length (Wright and Rausch, 1955).

Other measurements were based on systematic studies by King (1980) on the weasel (Mustela erminea) and by Buchalczyk and Ruprecht (1977) on the polecat (Mustela putorius). Wolverine studies by Goldman (1935), Cowan (1936), Flook and Rimmer (1965), and Youngman (1975) assisted in selection of cranial measurements. Most of the descriptions of measurements in Tables 2 and 3 are standard and according to DeBlase and Martin (1974).

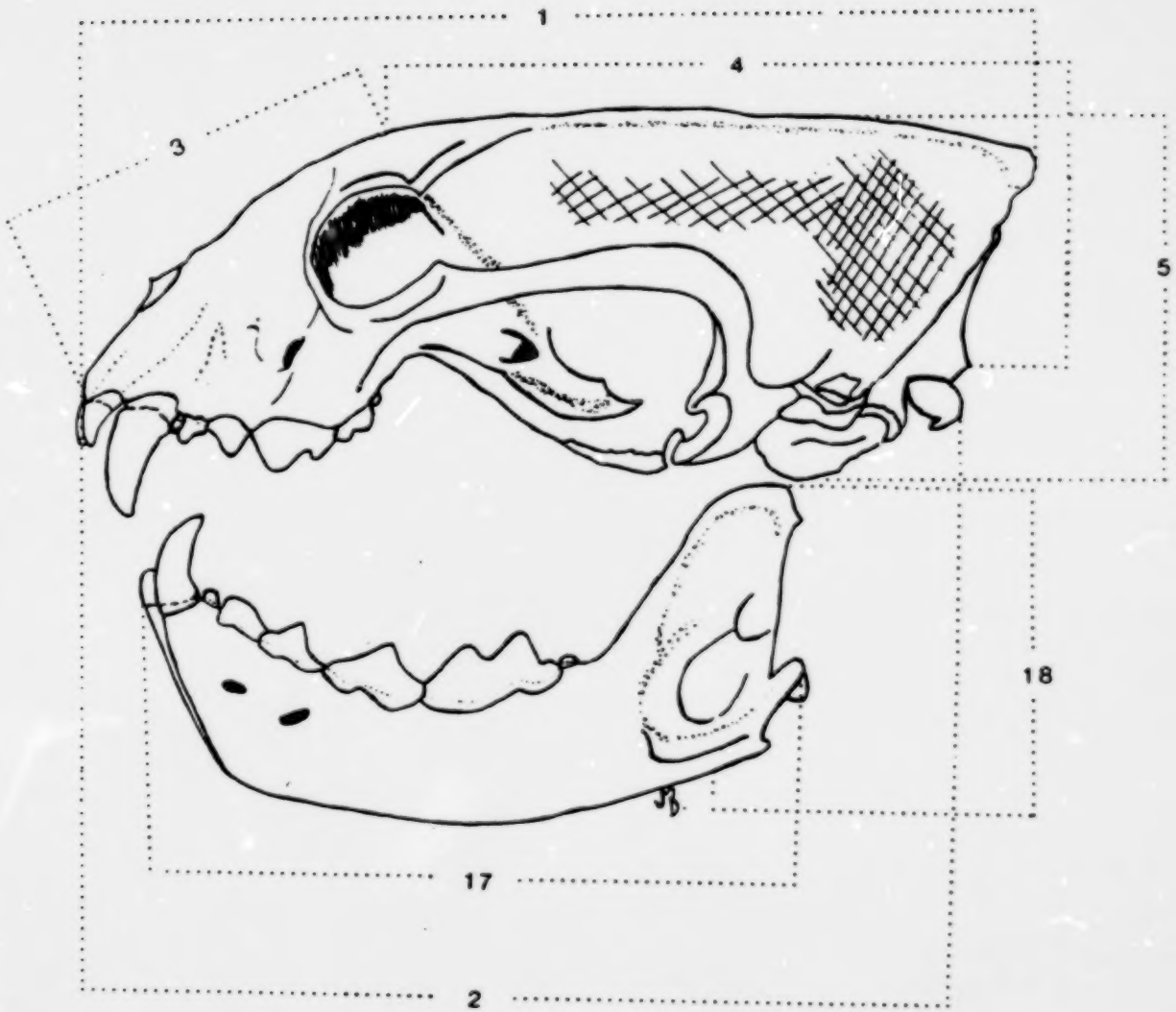


Figure 3. Lateral view of the wolverine skull depicting cranial measurements (Table 2). #GG-79-1 (Yukon Department of Renewable Resources) (female, 1979) drawn lifesize.

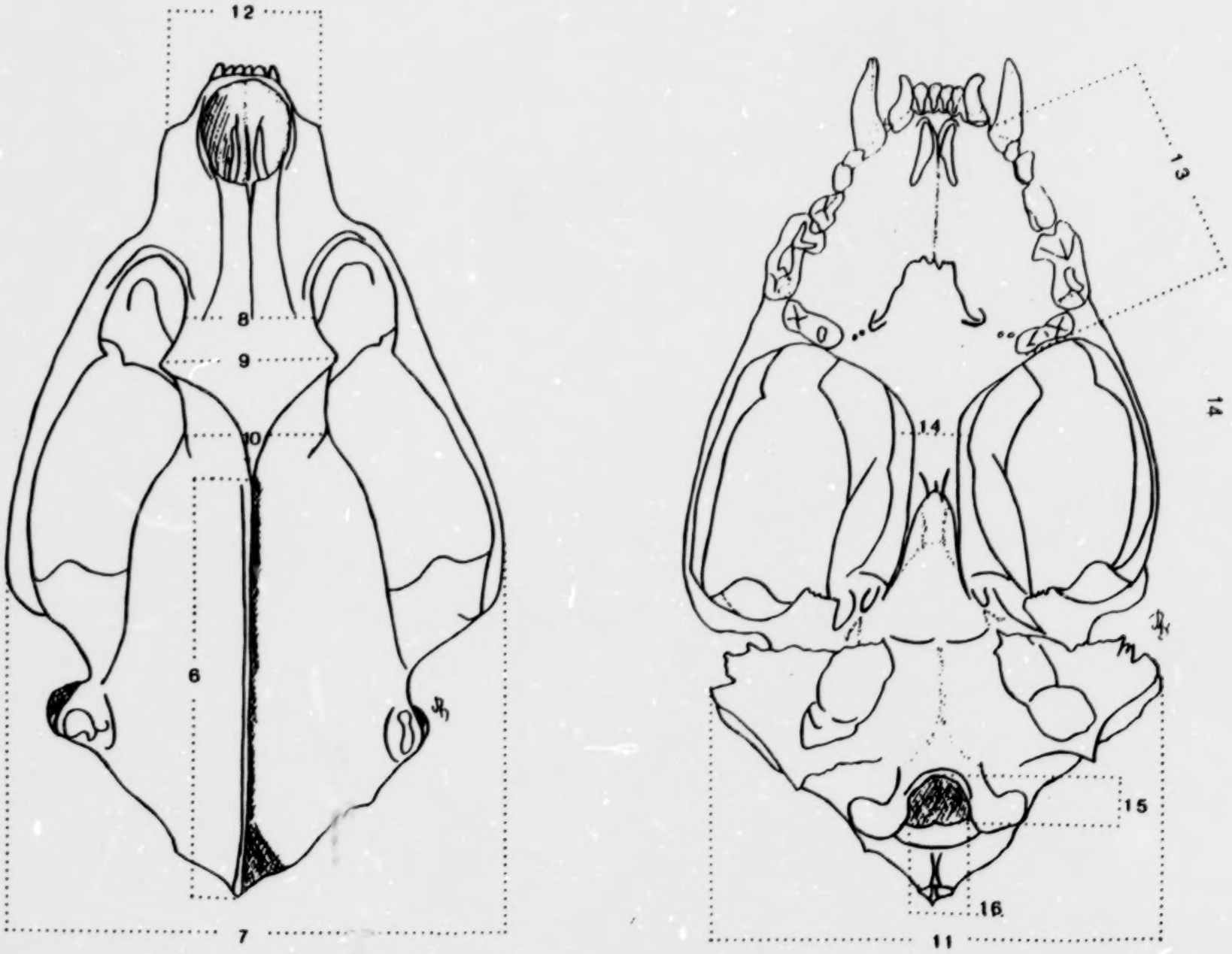


Figure 4. Dorsal and ventral views of the wolverine skull

Table 2. Cranial Measurements

Number		Measurement
1	LSK	greatest length of skull from the most anterior part of the rostrum (excluding teeth) to the most posterior part of the skull
2	CBL	condylobasal length from the anterior edge of the premaxillae to the posterior-most projection of the occipital condyles
3	VCL	viscerocranium length from the most anterior part of the rostrum to the least interorbital breadth
4	BCL	braincase length linear distance from the least interorbital breadth to the foramen magnum
5	BCH	braincase height from the auditory bullae to the top of the saggital crest
6	LSC	length of saggital crest
7	ZYB	zygomatic breadth greatest distance between the outer margins of the zygomatic arches
8	IB	least interorbital breadth least distance dorsally between the orbits

9	ECB	ecto-orbital breadth greatest width across the post-orbital processes
10	PB	post-orbital breadth least distance across the skull posterior to the post-orbital processes
11	MB	mastoid breadth greatest width of skull including the mastoids
12	RB	rostrum breadth width of the rostrum taken at the alveoli of upper canines
13	MXL	maxillary toothrow length length from anterior edge of alveolus of upper canine to posterior edge of alveolus of last tooth
14	PC	palatal constriction least distance across the palate
15	FMW	foramen magnum width interior width
16	FML	foramen magnum length interior length
17	MDL	mandible length length of the mandible from anterior edge of alveolus of canine to the posterior-most projection
18	HRM	height of ramus mandibulae

19	OS%	% suture obliteration relative measure based on % suture closure (primarly internasal and zygomatic)
20	EXT	saggital crest extension length of skull minus condlyobasal length

Table 3. Canine Measurements

Number		Measurement
1	CLL	lower canine length distance from the edge of the alveolus to the tip of the canine at the center of the lateral surface
2	CLU	upper canine length (as above)
3	CDU	upper canine diameter anterior-posterior diameter at the alveolus
4	CDL	lower canine diameter (as above)
5	ENUP	mean enamel line distance distance from the enamel line to the edge of the alveolar socket at the center of the lateral surface (averaged for upper canines)
6	ENLO	mean enamel line distance (as above, averaged for lower canines)

3.3 Age Determination

The enamel line technique was developed by Churcher (1960), who successfully correlated enamel line distances with known age for both upper and lower canines in red fox (Vulpes vulpes). Allen (1974) confirmed the technique's accuracy for this species. Nellis et al. (1978) successfully used it to age coyote (Canis latrans) with a slight adjustment because of differences in the coyote skull. Laura Friis (personal communication, 1982) is currently attempting to use the method to age wolves. Aging wolverines has not been attempted with this method.

The rationale behind the enamel line technique is discussed by Allen (1974) and summarized here. Canines progressively acquire cementum deposits at the roots while the cusps are simultaneously worn down. The canine itself changes little in length. However, any fixed point on the tooth's surface will move away from the alveolus and towards the outer tip. Therefore, the proximal edge of the enamel line forms a determinable fixed point. The distance between it and a standard point on the edge of the alveolus is related to the age of the individual. Details of the actual measurement follow Allen (1974).

It was also desirable to identify cranial dimensions that can be used as indicators of age. Age determination in wolverine is poorly documented and availability of an aged skull series presented the opportunity to investigate this aspect.

Myhre (1968) used ossification of cranial sutures to estimate age. This was also proposed by Wright and Rausch (1955) and evaluated by Rausch and Pearson (1972). Wright and Rausch (1955) noted that in the adult male wolverine the saggital crest extends posteriorly further than in immatures and may be used as an indication of age. The relationships between absolute age and the above measurements, as well as all others taken, were examined.

Aged skulls were put into age classes of juvenile (0-1 years), subadult (yearling) (1-2 years), and adult (3+ years) according to Liskop et al. (1980). The same comparisons between cranial dimensions and absolute age were repeated with age class.

3.4 Analysis

All statistical analyses were done with the Statistical Package for the Social Sciences (SPSS) as supported by the Computing Center at Simon Fraser University. Means, standard deviation, standard error, variance, maxima, minima, and ranges were calculated for all variables. Frequency histograms were used to examine distributions of the data. Comparisons to normality were made by calculating kurtosis and skewness. Sexes were treated separately in all analyses due to size differences but pooled to increase sample size in the age analyses.

3.4.1 Correlations with Cranial and Canine Measurments and Age

Scattergrams of all variables with age reveal no linear relationship for any variable. Hence, a non-parametric rank correlation method, Kendall's tau, was used for analyses with absolute age.

Means for each variable in each of the three age classes were compared using one-way analysis of variance and Scheffe's test ($P \leq .05$) (Sokal and Rohlf, 1969). Homoscedasticity was checked by Cochran's C, Bartlett-Box and the maximum variance/minimum variance tests (Sokal and Rohlf, 1969).

3.4.2 Discriminant Function Analyses

Inter-regional and inter-sex comparisons were made with a multivariate analysis technique, linear discriminant functions, as part of the SPSS package. Details of the procedure are from Nie et al. (1975) unless otherwise indicated.

The method is well established but until recently biological applications were uncommon. Jolicoeur (1959) used an analogue of discriminant functions, canonical analysis, to analyze geographic variation in the wolf. Lawrence and Bossert (1967) clearly distinguished wolf, coyote and dog species by linear discriminant analysis. Elder and Hayden (1977) attempted to discern the validity of the approach and achieved full separation of coyotes, dogs and gray wolves despite lack of uniformity within the species. Huson and Page (1979) obtained between 66% to 88% correct classification in a study of inter-sex and inter-regional

differences, respectively, in cranial measurements of red fox. Discriminant analysis has also been successfully used by Diersing and Wilson (1980) and Diersing (1981) in systematic studies of rabbit, Sylvilagus. Jeffers (1977) proposed an ecological classification based on discriminant functions. Foottit and Mackauer (1980) analyzed the effectiveness of discriminant analysis in distinguishing between 18 populations of balsam wooly aphid (Adelges piceae).

In short, the method finds the weighted sum of a number of characteristics (discriminating variables) which is most different for two or more populations, ie., that which best separates the samples (Lawrence and Bossert, 1976). The weighted sums are the discriminant functions and the weights are known as the discriminant coefficients.

Selection of discriminating variables was either direct: all variables are included simultaneously, or through the step-wise method. In the latter, independent variables are selected for entry into analyses on the basis of their discriminating power. A reduced set of variables is found which is almost as good as and sometimes better than the full set. Murray (1977) cautions that the stepwise method may be inefficient in variable selection. However, this occurs only when more than two groups are being compared (Murray, 1977) and Huson and Page (1979) acknowledge that no generally superior technique is known.

The criterion chosen to control variable selection was the Mahalonobis D^2 statistic, which seeks to maximize the distance between the two closest groups. Rao (1952) notes that the D^2 statistic is a useful measure of multiple character differences between two populations.

The method forms one or more linear combinations of discriminating variables, known as the discriminant functions. These functions take the form:

$$D_i = d_{i1} X_1 + d_{i2} X_2 + \ldots + d_{ip} X_p$$

where

D_i = score for the discriminant function i

d_{ip} = standardized discriminant coefficients

X_{ip} = standardized values of the p discriminating variables

The maximum number of functions is equal to the number of groups minus one or the number of discriminating variables, if the number of groups exceeds the number of variables. Discriminant functions can be regarded as axes of geometric space and used to study the spatial relationships of groups by plotting one function against the other and locating individuals within the grid. If only one function exists, a frequency histogram can be derived.

Two statistical tests were applied to measure the success of discrimination. Eigenvalues and their associated canonical correlations relate the ability of each function to separate the groups. Wilk's lambda is an indication of the amount of discriminating power actually being used.

Group centroids, the mean discriminant scores for each group on the discriminant function, were calculated. Comparison of centroids indicates how far apart the groups are along that dimension.

The standardized discriminant function coefficients represent the absolute values of the contribution of each variable to the discriminant function. Signs of coefficients indicate the nature of differences between variables.

Classification is the second part of the discriminant technique, analysis being the first. Classification functions are derived from the pooled within-groups covariance matrix of the centroids and then used to either recheck the original discriminations or to classify new cases with unknown memberships.

3.4.2.1 Inter-sex Comparisons

The objectives were:

i. to determine the nature of differences in cranial dimensions

between males and females

ii. to classify unsexed individuals and include them in further analyses

The latter was especially relevant in increasing the sample size of the Vancouver Island sample. One of the Island specimens (BCPM 1570) was omitted from the analyses as its condition prevented many measurements from being taken. Sexes were compared using the stepwise variable selection method, separately for the three populations. The samples were then reclassified to check for accuracy and unknowns were assigned sex on the basis of the classification procedure. These individuals were then included in further analysis. Stacked histograms were derived by plotting frequency of individuals against their respective function for the three samples.

7.1.2.2 Inter-regional Comparisons

All three populations were simultaneously compared using the direct variable selection method. The best set of discriminating variables was found by eliminating those that contributed little to their respective functions. The effect on the separation of group centroids and the success of re-classification was the criteria for removal. One function was then plotted against the other and individuals located within this spatial grid. Location of group centroids was also noted.

4 RESULTS

4.1 Age Determination

Results are summarized for correlations with absolute age (Table 4) and with age class (Table 5) for male, female and pooled samples. 95% confidence intervals for variables with significantly different means between age classes are given in Table 6.

Standardized discriminant function coefficients and canonical correlations for Mainland, Yukon and Island intersex comparisons are given in Tables 7, 8 and 9, respectively. Summaries of centroid values and classification results are given in Tables 10 and 11.

Stacked frequency histograms were derived for Mainland (Figure 5), Yukon (Figure 6) and Island (Figure 7) samples.

Standardized discriminant function coefficients along with the percent variability and canonical correlations for the associated functions in the inter-regional comparisons are summarized for males (Table 12) and females (Table 15). Centroid values and classification results are given for males (Tables 13 and 14) and females (Tables 16 and 17).

Scatterplots of one discriminant function against the other were derived for male (Figure 8) and female (Figure 9) inter-regional comparisons.

Table 4. ρ values (sample size, n; significance, P) for correlations of cranial and canine measurements with absolute age in male, female and pooled samples

Variable	Male (n, P)	Female (n, P)	Pooled (n, P)
ENUP	0.3812 (20, .014)	0.6422 (12, .004)	0.4247 (32, .001)
ENLO	0.2951 (18, .054)	0.3599 (10, .096)	0.3375 (28, .011)
CLU	0.3003 (15, .076)	0.5217 (9, .043)	0.3779 (24, .011)
CLL	0.3213 (12, .086)	0.5960 (7, .053)	0.3367 (19, .035)
OSS	0.4976 (18, .008)	0.5265 (11, .029)	0.5078 (29, .013)
LSC	0.3118 (16, .054)	-0.0412 (8, .447)	0.2597 (24, .048)
EXT	0.3726 (17, .024)	0.3719 (9, .100)	0.4287 (26, .002)
LSK	0.3687 (18, .021)	0.1680 (10, .269)	0.3168 (28, .014)
ECB	0.5580 (16, .003)	0.1995 (11, .218)	0.3964 (27, .004)
CEL	0.3577 (20, .019)	-0.0527 (10, .423)	0.2316 (30, .049)
CYB	0.5779 (19, .001)	0.1384 (10, .305)	0.3362 (29, .009)
IB	0.5558 (19, .001)	-0.0183 (12, .470)	0.3609 (31, .005)

CDL	0.2331 (18, .109)	0.6973 (11, .003)	0.3133 (29, .016)
CDU	0.0889 (20, .306)	0.3328 (12, .087)	0.1600 (32, .122)
FML	0.3732 (15, .039)	0.8246 (8, .006)	0.4031 (23, .008)
FMW	0.3353 (15, .054)	-0.4125 (8, .096)	0.2244 (23, .008)

Table 5. One-way analysis of variance, Scheffe's test, ($P<0.05$) and sample sizes (n: juvenile(J) -subadult(S)-adult(A)) for correlations of cranial and canine measurements with age class in male, female and pooled samples. Age classes with significantly different means are indicated

Variable	Male	(n)	Female	(n)	Pooled	(n)
ENUP	——	(6-7-7)	——	(4-6-2)	J-A	(10-13-9)
ENLO	——	(6-5-7)	——	(4-5-1)	J-A	(10-10-8)
CLU	——	(5-7-3)	——	(4-5-0)	——	(9-12-3)
CLL	——	(5-4-3)	——	(4-3-0)	——	(9-7-3)
OSC	J-A	(5-5-8)	——	(3-6-2)	J-A	(8-11-10)
LSC	J-A	(4-4-8)	——	(2-4-2)	——	(6-8-10)
EXT	——	(4-5-8)	J-S	(2-5-2)	J-A	(6-10-10)
ZYB	J-A S-A	(6-5-8)	——	(2-6-2)	J-A S-A	(8-11-10)
IB	J-A	(6-6-7)	——	(4-6-2)	J-A	(10-12-9)
ECB	J-A	(6-4-6)	——	(3-6-2)	J-A	(9-10-8)
CHL	——	(6-6-8)	——	(3-5-2)	——	(9-11-10)
LSK	——	(4-5-9)	——	(2-6-2)	——	(6-11-11)
[illegible]	S-A	(5-4-8)	——	(2-5-2)	——	(7-9-10)
CDU	——	(6-7-7)	——	(4-6-2)	——	(10-13-9)
CDL	——	(6-6-6)	J-A	(4-5-2)	——	(10-11-8)
FML	——	(4-5-6)	J-S J-A	(2-5-1)	J-A	(6-10-7)
FMW	——	(4-5-6)	——	(2-5-1)	——	(6-10-7)

Table 6. 95% confidence intervals (mm and % for OS%) for variable means from significantly different age classes regarding cranial and canine measurements (J=juvenile, S=subadult A=adult)

Variable	Age Class	Male	Female	Pooled
ENUP	J			0.85 - 3.04
	A			2.80 - 4.61
ENLC	J			0.43 - 1.81
	A			1.47 - 3.05
OS%	J	17% - 100%		28% - 90%
	A	96% - 100%		97% - 100%
ISC	J	58.45 - 79.92		
	A	76.48 - 83.08		
EXT	J		0 - 18.48	5.43 - 15.82
	S		10.89 - 13.18	
	A			13.55 - 20.15
ZYB	J	95.48 - 103.97		94.41 - 101.91
	S	96.63 - 106.66		92.96 - 100.91
	A	104.89 - 111.22		101.05 - 110.04
IB	J	36.39 - 40.35		37.22 - 39.32
	A	40.74 - 43.69		39.57 - 43.07
ECB	J	43.29 - 47.22		43.90 - 46.25
	A	47.63 - 52.17		46.85 - 51.15
BCL	S	91.42 - 104.60		
	A	102.53 - 110.03		
CDL	J		7.75 - 8.47	
	A		4.74 - 13.00	
FML	J		15.41 - 16.04	15.84 - 18.04
	S		16.37 - 17.23	17.53 - 19.23
	A		(1 adult)	

Table 7. Standardized discriminant function coefficients for the discriminant function calculated from Mainland males (n=10) and females (n=11)

Variable	Coefficient
PB	-0.66902
ECB	-0.80658
MXL	-0.79192
RB	1.38008
HRM	0.76978
PC	0.48596
Canonical correlation	0.9210241

Table 8. Standardized discriminant function coefficients for the discriminant function calculated from Yukon males (n=3) and females (n=3)

Variable	Coefficient
MB	12.18626
RB	3.27743
BCH	18.40184
PC	-28.49889
Canonical correlation	0.9995942

Table 9. Standardized discriminant function coefficients for the discriminant function calculated from Island males (n=3) and females (n=2)

Variable	Coefficient
MB	8.26119
VCL	2.49075
PC	-6.31096
Canonical correlation	0.9994718

Table 10. Discriminant functions evaluated at group means (centroids) for inter-sex comparisons

Region	Male (M)	Female (F)	(M-F)
Mainland	2.35896	-2.14451	4.50347
Yukon	28.65221	-28.65221	57.30442
Island	19.45021	-29.17531	48.62552

Table 11. Classification results for inter -sex comparisons

Region	Male	Female	Total
Mainland	24/30 (80%)	18/19 (94.7%)	85.7%
Yukon	7/7 (100%)	5/5 (100%)	100%
Island	3/3 (100%)	2/2 (100%)	100%

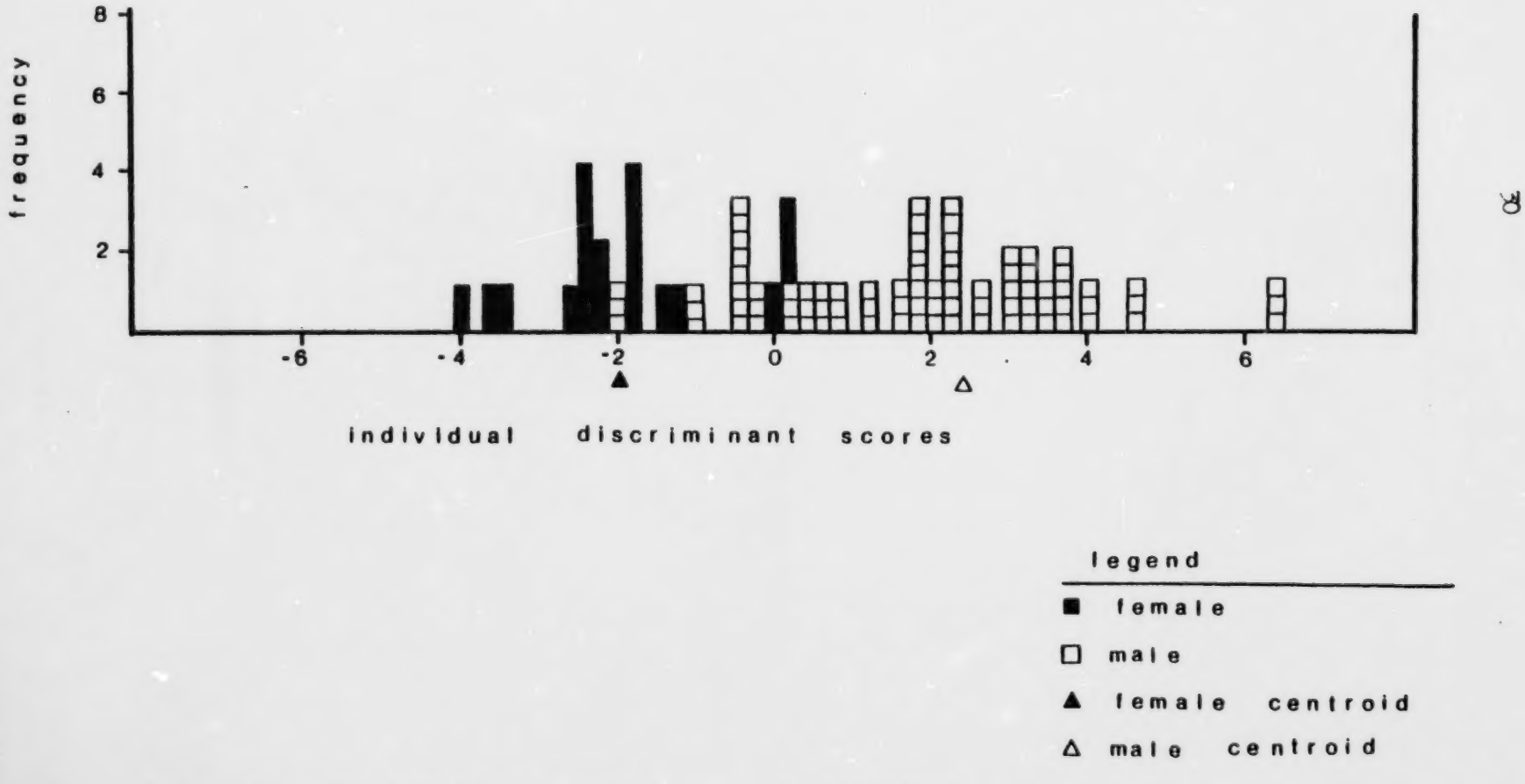


Figure 5. Stacked frequency histogram of individual

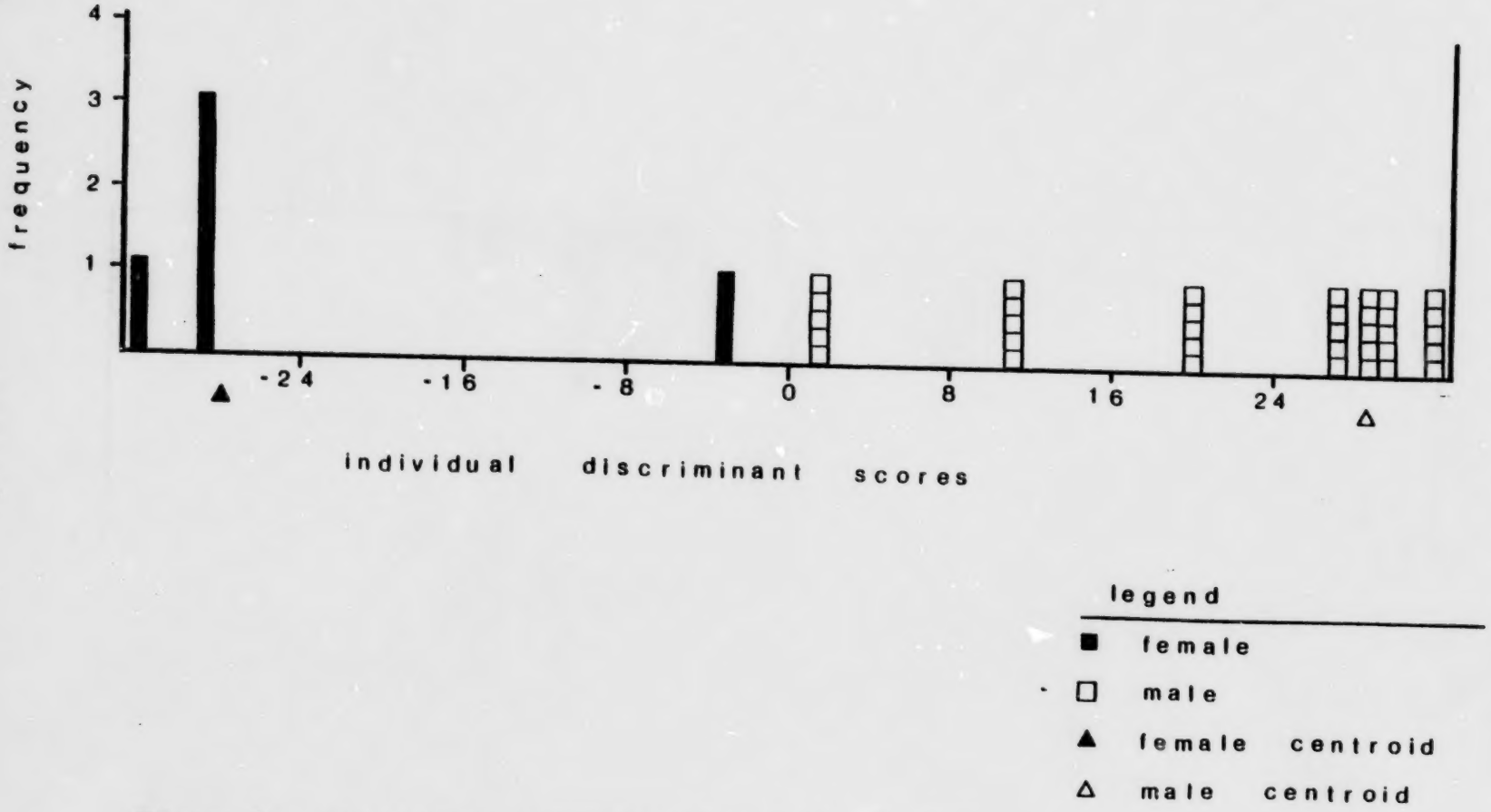


Figure 6. Stacked frequency histogram of individual discriminant scores for Yukon sexes.

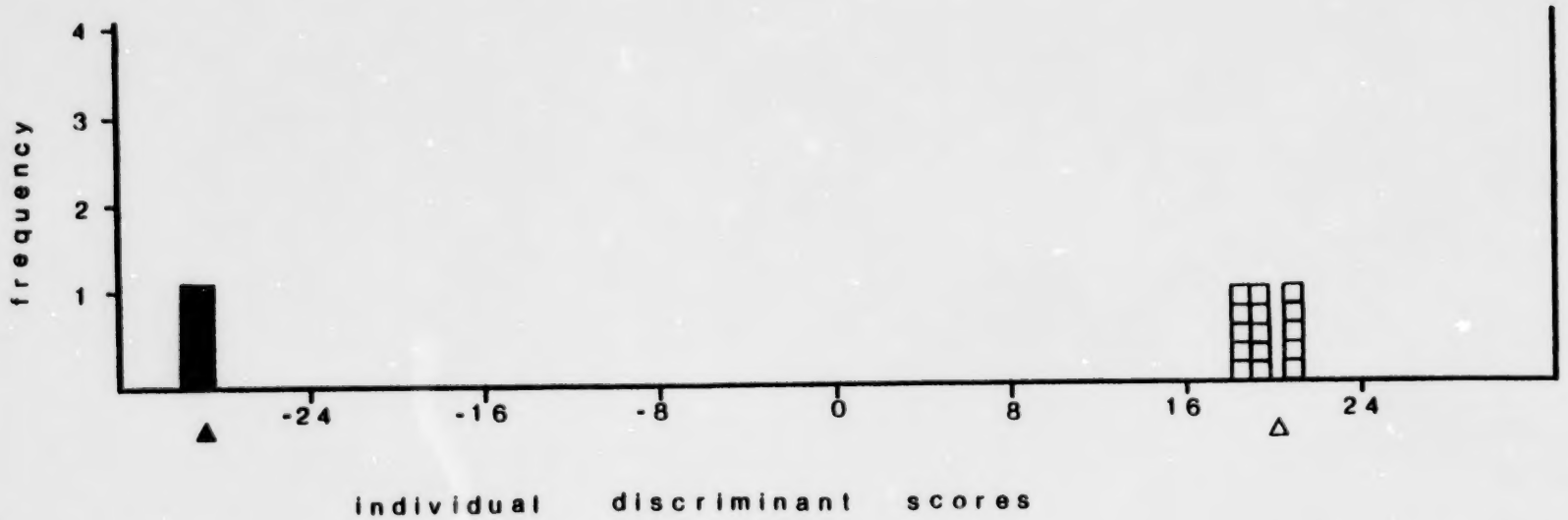


Figure 7. Stacked frequency histogram of individual discriminant scores for Island sexes.

Table 12. Standard discriminant function coefficients for the two discriminant functions calculated from Mainland (n=14), Yukon (n=2), and Island (n=4) males in inter-regional comparisons

Variable	Discriminant function I	Discriminant function II
ZYB	-1.67744	0.72109
PB	0.28453	-0.08820
MB	1.25020	-0.22883
VCL	-1.75072	-1.34203
RB	2.39792	0.92857
PC	0.07162	1.25469
CDU	3.12221	1.60831
CDL	-1.86284	-1.25680
IB	-1.94442	-1.60696
MXL	0.66421	0.57506
Relative variability	72.09%	27.91%
Canonical correlation	0.8677876	0.7358243

Table 13. Discriminant functions evaluated at group means (centroids) for Mainland, Yukon and Island males in inter-regional comparisons

	function I	function II
Mainland	-0.98924	0.22631
Yukon	3.74270	1.89971
Island	1.59101	-1.74195

Table 14. Classification Results for Mainland, Yukon and Island males in inter-regional comparisons

		Predicted Group		
Actual Group	n	Mainland	Yukon	Island
Mainland	34	32 (94.1%)	2 (5.9%)	0 (0.0%)
Yukon	7	3 (42.9%)	3 (42.9%)	1 (14.3%)
Island	4	0 (0.0%)	0 (0.0%)	4 (100.0%)

Table 15. Standardized discriminant function coefficients for two discriminant functions calculated from Mainland (n=14), Yukon (n=5) and Island (n=3) females in inter-regional comparisons

	Discriminant function	
Variable	I	II
ZYB	0.3296	0.05935
IB	0.04216	1.33381
PB	1.71857	0.58442
ECB	0.79663	-1.47040
MB	-0.60101	-0.33064
VCL	-0.63445	0.66960
MXL	0.25217	0.47238
RB	-4.48585	-0.18047
HRM	-1.21545	-0.54061
PC	1.37989	0.02045
CDU	1.17291	0.63573
CDL	2.22192	-0.33869
Relative variability	88.35%	11.65%
Canonical correlation	0.9162698	0.6389624

Table 16. Discriminant functions evaluated at group means (centroids) for Mainland, Yukon and Island females in inter-regional comparisons

	function I	function II
Mainland	1.45512	0.24759
Yukon	-3.70507	0.46459
Island	-0.61543	-1.92976

Table 17. Classification Results for Mainland, Yukon and Island females in inter-regional comparisons

		Predicted Group		
Actual Group	n	Mainland	Yukon	Island
Mainland	24	21 (87.5%)	1 (4.2%)	2 (8.3%)
Yukon	7	0 (0.0%)	6 (85.7%)	1 (14.3%)
Island	3	0 (0.0%)	0 (0.0%)	3 (100.0%)

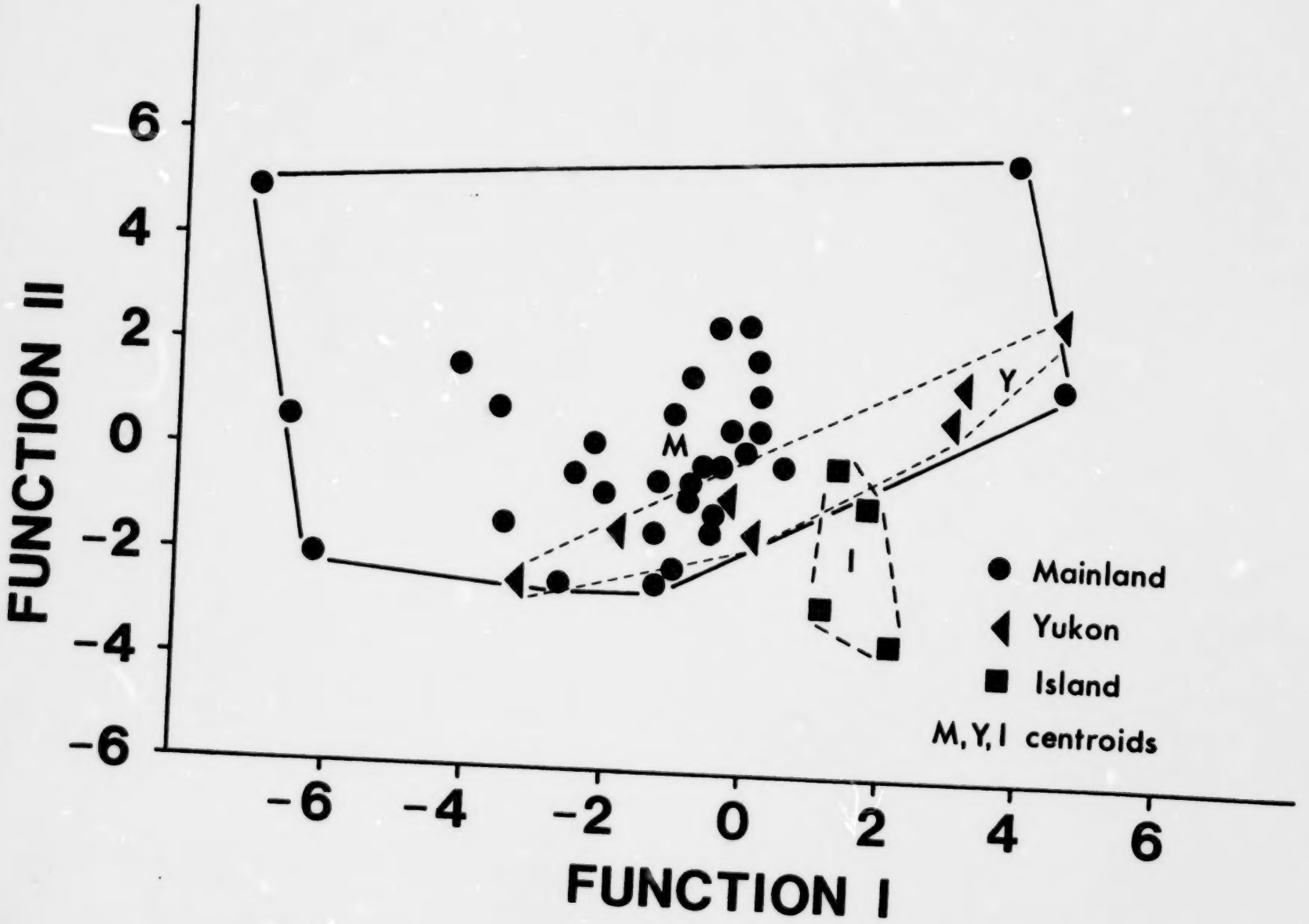


Figure 8. Scatterplot of two discriminant functions for Mainland, Yukon and Island males.

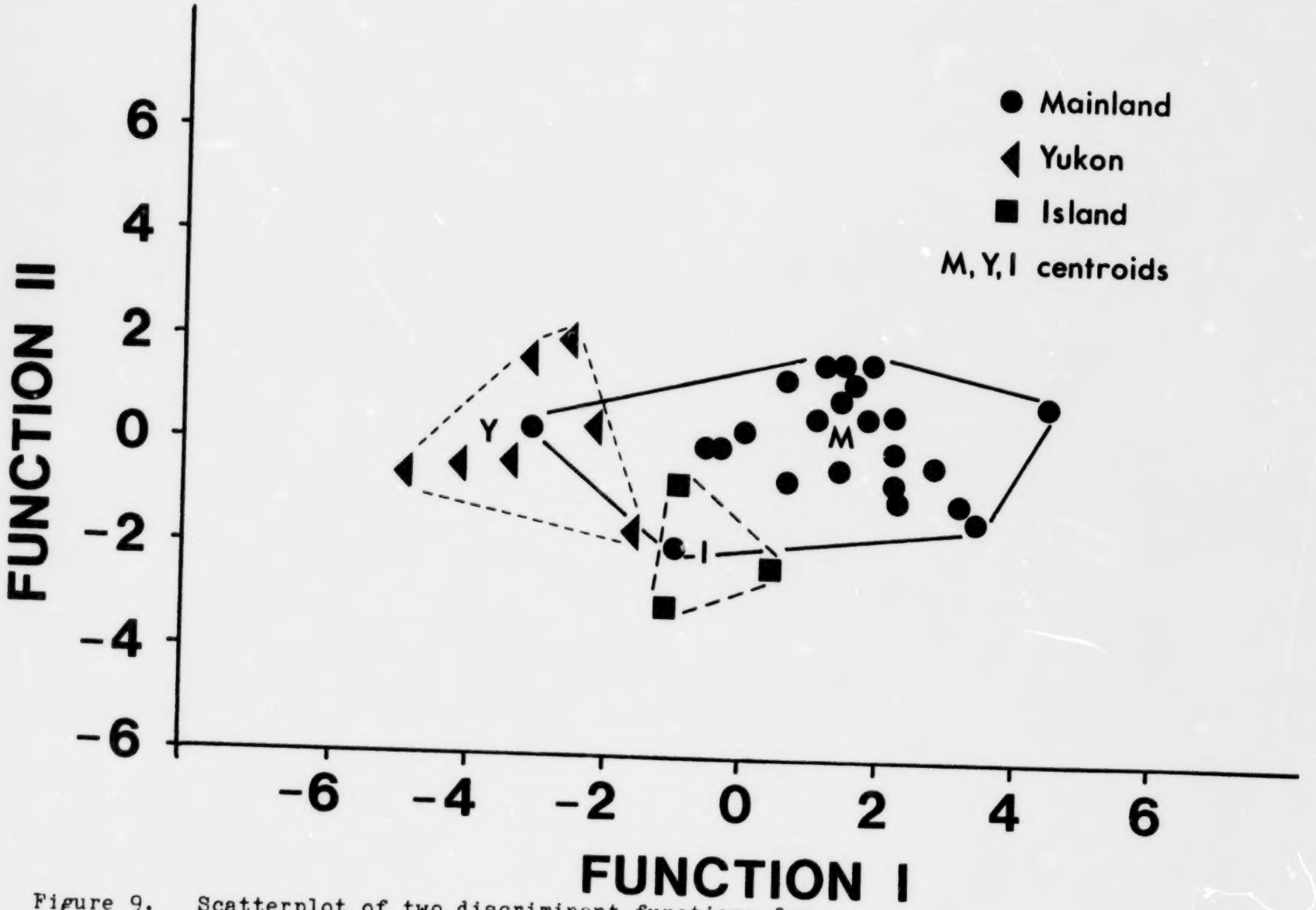


Figure 9. Scatterplot of two discriminant functions for Mainland, Yukon and Island females.

4.2 Abundance and Distribution

4.2.1 British Columbia Mainland

Quick (1953) reports that the center of wolverine population in western Canada appears to be near Fort Nelson. Records occur from the Peace River area (Sheldon, 1932; Cowan, 1939), although Cowan (1939) reports them as "rare" but more abundant than in the Rockies. Toner (1946) states that wolverine were occasionally noted in the lower Chilcotin River area of Cariboo district only before 1910. They are termed "rare" in the Atlin mountain region (Swarth, 1936) although more recent sightings are reported by Anonymous (Anonymous, 1975), Hogdson and Petrar (Hogdson and Petrar, 1979) and the BCPM (specimen 9994, 1977). Porsild (1945) finds wolverine rare in the Mackenzie delta. Earlier sightings are reported for the Lac La Hache area (Carl and Hardy, 1943), Driftwood valley region of north-central British Columbia (Stanwell-Fletcher and Stanwell-Fletcher, 1943), the Chilliwak district (Brooks, 1902), Paradise Mine area (Carl and Hardy, 1945) and Mt. Clemenseau (Tupper, 1962). Recent sightings are from Vaseaux Lakes (McKegney, 1976), Kitimat region (Hay, 1976), Gladys Lake (Carswell, 1975) and the Tatshenshini watershed (Demarchi, 1974).

Parks recording wolverine sightings are Yoho (Ulke, 1923, "not common"; Ulke, 1936), Kootenay (Munro and Cowan, 1944), Glacier (Bailey and Bailey, 1918; Munro, 1945), Mt. Revelstoke (BCPM records 1943, 1981; Cowan and Munro, 1944-46, Holbrow, 1976), Mt. Assiniboine (Parkin and Gunville, 1974; Holbrow, 1976), Mt. Edziza (Hazelwood, 1978), Spatsizi (Hodgson, 1976; Osmond-Jones et al., 1977; Bergerud and Butler, 1978), Manning (Bandy, 1952), Mt. Robson (Butler, 1972; Cannings, 1973), Well's Gray (Martin, 1950; Ritcey, 1952a, 1952b, 1954, 1955, 1958; Ritcey and Edwards, 1958; Grass, 1971; Cannings, 1977), Bowron Lake (Hall, 1934; Runyan, 1971; Ellington, 1973; Dyer, 1974), Tweedsmuir (Low, 1965; Hazelwood, 1975, 1976, 1977; BCPM records, 1975), Shuswap (Stirling, 1961), and Tatlatui (Osmond-Jones et al., 1977; Hazelwood, 1979). Edwards and Cowan (1957) write that wolverine display a "clinal trend" with an almost constant decrease from northwest to southeast in the boreal forest region of British Columbia. Highest fur production is reported on the high cold plateau in the northwest, with lower production for the Liard forest mountain area and still lower on the forested plains east of the mountains (Edwards and Cowan, 1957). No evidence of

wolverine was found on the Queen Charlotte Islands (Osgood, 1901; Foster, 1965).

Holbrow (1976), whose results are summarized in this paragraph, presents trapping and sighting data which show a wide and dispersed distribution. He notes that only the Prince George area reported in excess of 20 wolverine trapped in 1974-75 and 1975-76. Eight areas caught 14 or more over the same time period; Terrace, Hazelton, Germanson Landing, Fort St. John, Stewart, Mackenzie and Dawson Creek. Several centers had less than 14: in declining importance, Chetwynd, Smithers, Burns Lake, Vanderhoof, Fort St. James and Pink Mountain. From interviews with trappers Holbrow found none had captured more than 30 wolverine and those were generally dispersed throughout the province. Two trappers indicated they had caught more than 100 in the regions west of Jasper and east of Juneau on the Alaska - British Columbia border. The former agrees with my trapping and sighting data as an area of high occurrence (Fig. 10). Holbrow also indicates the following areas as those of common sightings from 1970 to 1975: Cassiar Mountains, Liard River, Ospika River (also found from my trapping data), Chilco Lake, northeast of Garibaldi Provincial Park, and the Nelson - Cranbrook - Sparwood area. Besides the Queen Charlotte Islands, Holbrow lists negative sighting areas as the central coast region, the adjacent small islands, the Chilcotin area in the interior, the Similkameen region and several south-eastern regions. I also did not obtain records of wolverine for these areas (Fig. 10).

Percentage of provincial populations by region and according to the Fish and Wildlife branch (1979) are >40% - Omineca Peace; 25% - Skeena; 18% - Cariboo; 9% - Kootenay; 4% - Thompson-Okanagan; and 3% - Lower Mainland. Similar percentages were obtained from my data from trapping locations; 41%, 30%, 15%, 7%, 4% and 3% for the above respective regions (Appendix 2). My findings agree with those of Holbrow in that wolverine in British Columbia appear to be of general distribution. An examination of Figure 10 reveals concentrations along the major highways. This is expected as trapping and sighting data would depend on accessibility of an area.

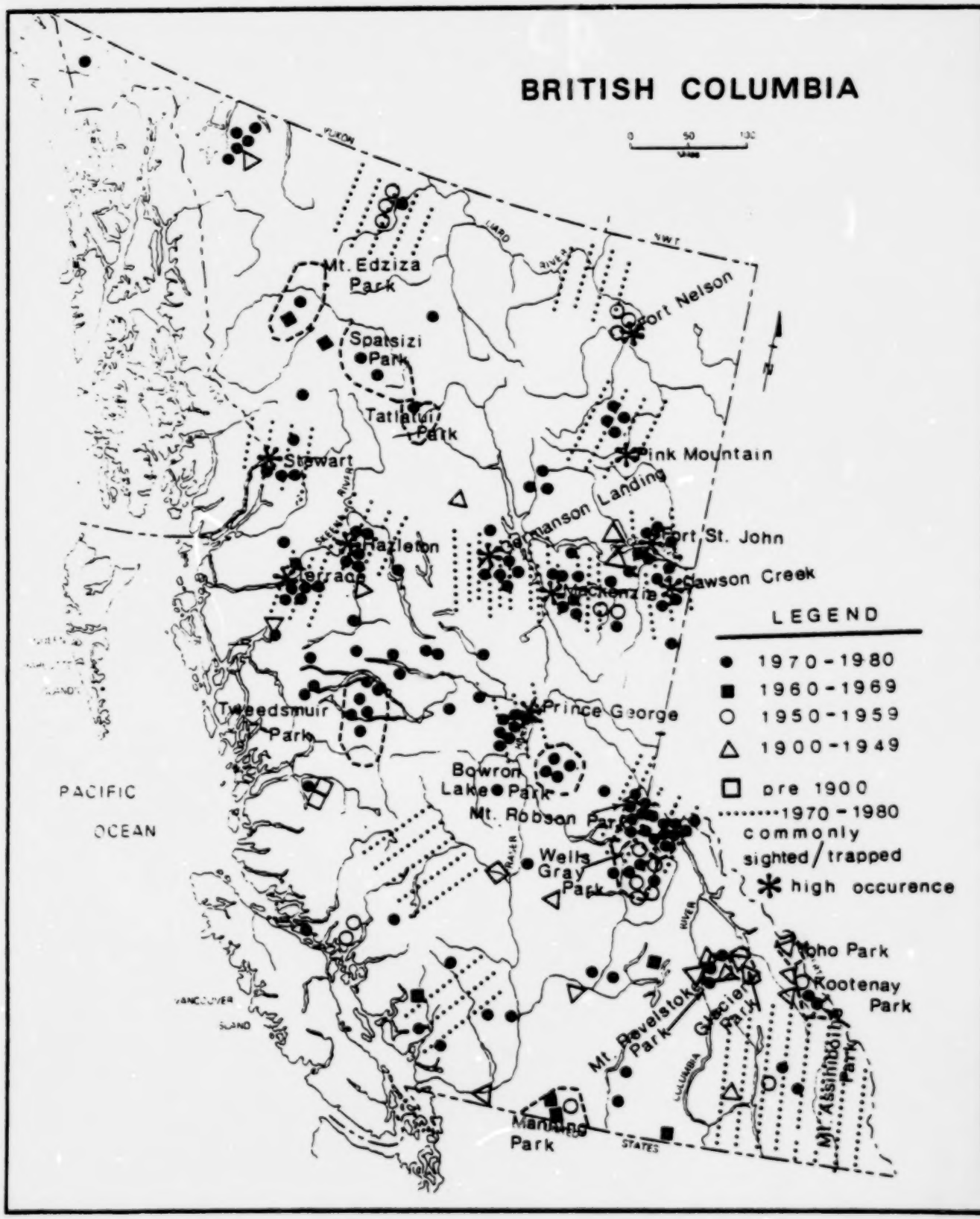


Figure 10. Distribution of Gulo gulo in British Columbia compiled from sightings, trapping locations and data in Holbrow (1976).

4.2.2 Vancouver Island

Distribution of wolverine on Vancouver Island (Fig. 11) was established from trapping locations of known specimens, personal communications regarding both sightings and trappings, reports in the literature and BCPM records. A listing of all reports and their sources is found in Appendix 3.

The majority of trappings occur from 1900 to 1949 and reports are scarce for more recent years. Most common areas where wolverine have been trapped are the Nimpkish River, Central Lake and Malahat - Jordan River areas (Bud Frost, personal communication). One Indian trapper is reported to have caught 12 or so in his trapping career (pre 1950) around Central Lake (Bud Frost, personal communication). Swarth (1912) reports that the Indians of Friendly Cove would bring in 1 or 2 a year.

The most recent specimen (BCPM 9872, Rooney Lake) dates from 1978, an animal in poor condition and found by chance (Fish and Wildlife, Nanaimo, personal communication). Seven sightings are reported for the period of 1973 - 1981, the most recent being in October of 1981 at Lake Cowichan (Fish and Wildlife, Nanaimo, personal communication).

Few reports of more than one animal occur. A female and 4 kits were sighted around Nimpkish River (1968-69, Bud Frost personal communication) and a female and 2 kits were observed south of Mt. Joan (1975, Fish and Wildlife, Nanaimo, personal communication).

Other evidence of wolverine is occasionally reported. Ken Hallberg (personal communication) observed "quite a few" tracks in the winter of 1932 south of the Nanaimo River and Skate Hames (personal communication) recalls seeing tracks at the head of the Oyster River in the 1930's and reports finding a den in the 1940's on Constitution Hill. The conservation officer at Campbell River (Pat Browne-Clayton, personal communication) receives a few reports of tracks every 1 or 2 years, mostly in the Nimpkish and upper Eve River areas.

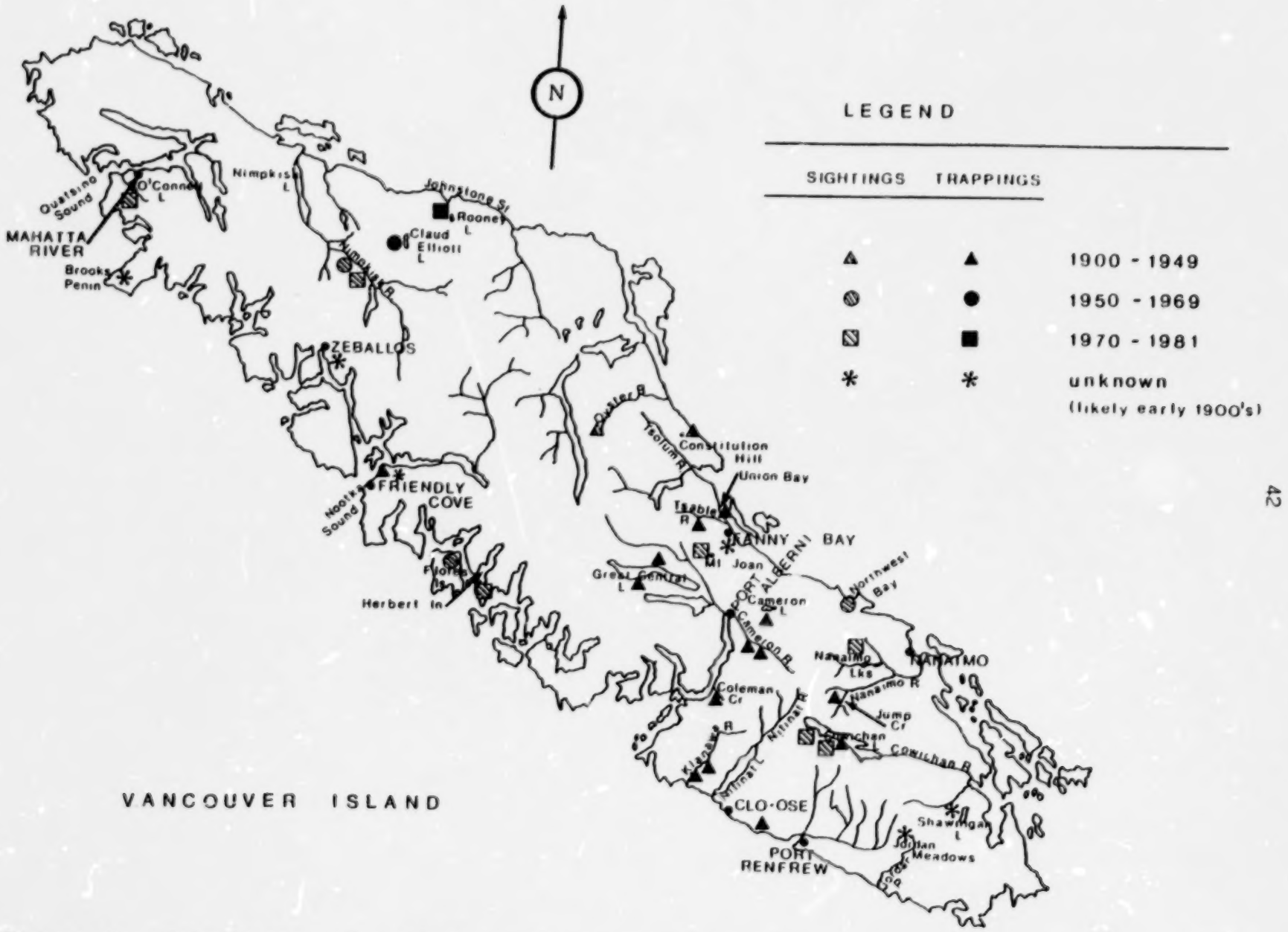


Figure 11. Distribution of wolverine on Vancouver Island from sightings in the literature, trapping locations of existing specimens and interviews.

5 DISCUSSION

5.1 Abundance and Distribution

5.1.1 British Columbia Mainland

van Zyll de Jong (1975) reports changes in wolverine abundance are much less pronounced in British Columbia than any other province, with a definite upward trend within the last 10 years. Seton (1909) and Cowan and Guiguet (1965) note that distribution of wolverine has been virtually unchanged since the turn of the century. Holbrow (1976) agrees with less pronounced changes in abundance and an overall high fur production rate. From 1919-20 to 1973-74 average yield per season was 235 wolverine, 1973-74 producing a maximum of 634 pelts and 1962-63 a low of 40 pelts (Holbrow, 1976). Increased fur production is evident since 1965-66 (Holbrow, 1976; Fish and Wildlife Branch, 1979). Harvests since the 1974-75 season have ranged from 142 to 508 wolverine per trapping period (Fish and Wildlife Branch, Victoria, personal communication). The low value of 142 occurred in 1979-80 and was a result of the harsh winter and decreased accessibility (Barry Saunders, personal communication). Two hundred twenty-five wolverine (0.1% of the total fur harvest) were taken in 1980-81 with an average value per pelt of $202.78 (Fish and Wildlife Branch, Victoria, personal communication).

The current provincial population estimate for wolverine is between 5,000 and 8,000, the lowest for any mustelid in British Columbia excluding sea otter and badger (Fish and Wildlife Branch, 1979). Frequency of field observations suggest wolverine occur at lower densities than other carnivores of comparable size (van Zyll de Jong, 1975). Kelsall (1968) reported an average of 8.5 wolves per wolverine in the Northwest Territories and Penner (1976) a ratio of 11.7 wolves per wolverine in the Athabasca tar sands region of Alberta. Reported densities for wolverine in Scandinavia are 1/200 to 1/500 km^2 (Krott, 1959) and in the U.S.S.R. 1/1000 km^2 (Teplov, 1955) and 1/780 to 1/5200 km^2 (Krott, 1959). Hornocker and Hash (1981) report an average density of 1 wolverine per 65 km^2 in Montana with average yearly ranges of 422 km^2 and 388 km^2 for males and females, respectively. The greater density is suggested to be a result of

the more plentiful food supply in the study area (Hornocker and Hash, 1981). Quick (1953) reports densities of about 1/210 km^2 for British Columbia based on returns from a registered trapline and Edwards and Cowan (1957) report densities of 1/610 to 1/24,000 km^2, also based on trapping data. Clearly there is need for more information on wolverine density in British Columbia.

5.1.2 Vancouver Island

Most reports (except one for Union Bay) occur in the insular mountain region of Vancouver Island and in relatively inaccessible and isolated areas (Fig. 11). Swarth (1912) notes "there are a few wolverines on the higher mountains of Vancouver Island, but they are rare and but very seldom trapped". More sightings/trappings were obtained for the southern portion of Vancouver Island (Fig. 11). Increasing settlement in this area probably explains both the frequency of earlier reports and lack of those more recent.

It is impossible to establish a population estimate. The general consensus is that wolverine on Vancouver Island are extremely rare. Scarcity of sightings can be explained by the animal's rarity, its elusive nature and inaccessibility of habitat. Increasing tourism and settlement, and the effects of logging activity may serve to decrease the effective range of wolverine on Vancouver Island and possibly adversely affect the existing population.

5.2 Variability, Normality of Data, Assumptions and Significance of Discriminant Functions

The common underlying assumption in all analyses is one of random samples. Most of the specimens were obtained by trapping. No bias is anticipated and resultant samples are assumed to be randomly selected. Rausch and Pearson (1972) report that sex ratios from catch statistics do not accurately depict true sex ratios, as males have greater ranges and are more likely to be trapped. As sexes were treated separately, this factor was not a problem.

With a few exceptions, coefficients of variation for all variables ranged from about 2% to 14%. However, the enamel line

measurements showed considerable variability with coefficients of variation ranging from 40% to 90% . Enamel line distances were only included in the correlations with age and no other analyses.

Males in the aged skull series ranged from 0.5 to 8 years of age with a mean of 2.6 and the females, 1 to 6 years of age with a mean of 2.1 years. It is reasonable to assume the unaged skulls have a similar age distribution as both were subject to the same sampling conditions. It was necessary to determine effect of age on cranial dimensions in order to ascertain whether separation according to age or age class was necessary. The low coefficients of variation for most of the measurements and lack of a strong correlation between any variable and absolute age both indicated that age contributed little to within-sample variability.

Frequency distributions along with the statistics of kurtosis and skewness indicated the data was more or less normally distributed. Analysis of variance assumes a random distribution, homoscedasticity and a normally distributed population (Schefler, 1979). Schefler (1979) notes that for analysis of variance, "it is generally agreed that reasonable departures from normality do not seriously affect the validity of the results". The tests for homoscedasticity indicated for the most part homogeneous variances.

The discriminant analysis technique assumes multivariate normality and equal variance-covariance matrices for the a priori groups (Ludwig, 1974). Testing for multivariate normality is involved and data transformation, if required, is an immense task (Ludwig, 1974). The problem can be circumvented as the technique is robust and minimizes irregularities resulting from violations of the assumptions (Blackith and Reyment, 1971).

Correlations with age class were noted for certain measurements, especially in distinguishing juveniles from adults. Eliminating all juveniles would have seriously reduced sample sizes. Three of the measurements correlated with age class, IB, ECB, and ZYB, appear in some sets of discriminating variables. The possible confounding effect of these variables was monitored by identifying those individuals mis-classified by the discriminant analysis.

Significances for the D^2 statistic in the inter-sex comparisons ranged from $P \leq 0.00001$ to $P \leq 0.0001$ for the Mainland, $P \leq 0.04$ to $P \leq 0.06$ for the Yukon and $P \leq 0.009$ to $P \leq 0.04$ for the Island samples. Considering a criterion of $P \leq 0.05$, all variable separations are significant. Significance of discriminant

functions is measured by the errors of misclassification (Kendall, 1972). Percent correct classification ranged from 80% to 100% except for Yukon males in inter-regional comparisons. Reasons are discussed below.

It may appear significant that 100% of the Vancouver Island sample was classified correctly in both inter-regional and inter-sex comparisons. However, the discriminant functions were derived from all individuals in the sample and then the same individuals were re-classified with classification functions derived from the original discriminant functions. In this case, degree of separation in regards to other groups is significant, not percentage of successful re-classification.

5.3 Age Determination

No strong correlations between any variable and absolute age occured for males or females (Table 4). There appeared to be a weak relationship with mean enamel line distance for upper canines with age in females. However, this may have been due to the small sample size (n=12). There was a weak relationship with increasing canine length and increasing age for both upper and lower canines in males. There was a slightly stronger correlation with greater significance in females. However, ρ values of only .52 and .60 were obtained for upper and lower canines, respectively. No trend was evident for both mean enamel line distances and canine length when the sample size was increased by pooling the two sexes.

Percent obliteration of sutures had correlation coefficients of at least 0.50 in the male, female and pooled samples. The cranial dimensions zygomatic breadth, ecto-orbital breadth and inter-orbital breadth exhibited correlations with age of at least 0.56 for males only. Neither length of saggital crest nor length of the saggital crest extension were significantly correlated with absolute age in males. Saggital crest extension is the only dimension that exhibited a slightly higher correlation when samples were pooled. Better correlations could not be achieved by increasing sample size, indicating sex differences were not confounding factors. Hence, results for pooled samples can be considered representative of the true populations.

Two interesting relationships were the significant positive correlations of 0.70 for lower canine diameter and age, and 0.82

for the length of the foramen magnum and age in females. Again, small sample sizes (11 and 8) may be responsible and these relationships were not apparent in either male or pooled samples. A larger sample size is necessary to confirm these correlations.

Neither lower nor upper canine mean enamel line distances distinguished between the three age classes for both sexes (Table 5). In the pooled sample, enamel line measurements significantly ($P \leq 0.05$) distinguished juveniles from adults. Increasing enamel line distance is a function of growth and unlikely to be correlated with sex. The correlation became apparent in the pooled sample due to an increase in sample size. However, in order to conclusively rule out sex differences, the method needs to be tested on larger samples of both males and females. An examination of the 95% confidence intervals (Table 6) reveals overlap between juveniles and adults. It would be difficult to classify those individuals with enamel line distances falling in the overlap region. Canine length could not separate age classes in male nor pooled samples. Female canine lengths were not compared as the sample did not contain adults, however similar results as for males are expected. If enamel line distance is correlated with age it is expected that canine length would remain the same because tooth wear is partially balanced by increasing cementum deposits at the roots (Allen, 1974).

The enamel line technique may have some use in distinguishing juveniles from adults but was not correlated with absolute age. The measurement can be difficult to take in situ as small distances are involved (<4 mm) and the enamel line is not easily detected. Application of this measurement to live animals would be even more difficult. It is doubtful the method will have future value as a field technique. There are simpler measurements that separate juveniles from adults and use of the enamel line technique as a means of estimating age in the wolverine is not recommended.

Certain cranial measurements distinguished adults from juveniles. These included length of saggital crest, interorbital breadth and ecto-orbital breadth in males; lower canine diameter in females; and length of the foramen magnum in the pooled sample. The latter distinguished juveniles from subadults and from adults for females. Neither condylobasal length nor total length of the skull alone separated age classes, therefore any ratios involving condylobasal length are redundant and are not considered.

Separation of subadults from juveniles or from adults was less clear. Positive results for foramen magnum length in females are doubtful as only 1 adult was included in the sample. Zygomatic breadth differentiated subadults from adults as well as juveniles from adults in male and pooled samples. However, some overlap occurs between confidence intervals for subadults and adults (Table 6). Wright and Rausch (1955) have proposed the saggital crest extension as an indicator of age in male wolverine. My analyses indicate this measurement can distinguish subadult and juvenile females but not males. In many male adult skulls the tendency towards a more posteriorly directed saggital crest was clearly visible and it was possible to correlate total saggital crest length with age class. Bell (1956) notes that bone lengths cannot be used as objective criteria of age. The rate and extent of development of saggital crests would be related to the size and work of jaw muscles inserted into them (Bell, 1956). My results show that for males saggital crest length can distinguish adults from juveniles and may be a quick method to estimate relative age. Saggital crest length will probably not be a useful dimension for aging females. If less than 10 mm in length, it may be used to classify juvenile females but with greater distances much overlap occurs (Table 6).

Braincase length distinguished male subadults from adults but not juveniles from subadults. Condylobasal length, taken on the same axis, does not discriminate between age classes. In addition, viscerocranium length (the adjunct to braincase length) also does not provide any discrimination. It is likely positive results for braincase length in males were anomalies of the small sample size (2 juveniles, 5 subadults and 2 adults).

Percent obliteration of sutures separated juveniles from adults for both male and pooled samples. It may also be applicable to females but was not evident due to the small sample size (3 juvenile, 6 subadult, 2 adult). Internasal and zygomatic sutures proved most useful. This was substantiated by Rausch and Pearson (1972) with the caution that even these sutures exhibited considerable variation. My results were also highly variable (Table 6). The only dimensions exhibiting no overlap in confidence intervals for juveniles and adults are zygomatic breadth (males), interorbital breadth (males and pooled sample), ecto-orbital breadth (males and pooled sample) and length of foramen magnum (females) (Table 6). It appears that these dimensions may provide clearer separation of adults and juveniles than do canine measurements or other cranial dimensions such as length of saggital crest and degree of suture closure.

The aging methods thus far considered are based on continuous traits, those which change throughout life and involve growth. Prior knowledge of an animal's allometric development with age is required and even then the result is usually broad, poorly defined age classes (Fleck, 1975). Differential or discontinuous traits are based on the seasonal cessation of active growth. Absolute age can be obtained and discrete age classes formed, but the techniques involved are often laborious and need specialized equipment (Fleck, 1975). Cementum analysis falls in this category.

A great variety of techniques have been utilized in attempting to age mammals. Morris (1972) provides a comprehensive review of mammalian age determination methods and King (1980) reviews methods for small mustelids. Klevezal and Kleinenberg (1967) prepared a comprehensive summary on the existence and use of annual layers in teeth and bone. All three papers comment on the difficulty involved in aging and the errors involved. Morris (1972) notes three major problems:

i. Any method must be checked for accuracy against specimens of known age and obtaining aged material is often difficult.
ii. Individual variation must be accounted for.
iii. The effect of genetic factors.

Improper analysis of data is a major source of error commented on by Dapson (1980).

Age determination in wolverine appears to be exceedingly difficult. Rausch and Pearson (1972) attempted to evaluate a number of methods. State of reproductive organs, closure of epiphyseal functions in long bones and ossification of cranial sutures were found adequate to separate young-of-the-year from older animals only if young less than 10-11 months old were considered (Rausch and Pearson, 1972). Weights of os bacula were used to distinguish young of the year from older animals but the method was not considered worthwhile for future studies (Rausch and Pearson, 1972). The value of lens weight as an aging technique was unclear due to insufficient sample size (Rausch and Pearson, 1972).

The wolverine skeleton develops rapidly for an animal of its size and the teeth mature rapidly (Rausch and Pearson, 1972). Wright and Rausch (1955) note that the skull of a juvenile male

at 4 months still has all his sutures open but is already as large in several measurements as that of an adult female skull. By at least 6 months, the majority of the sutures disappear, permanent dentition is present and in the male the saggital crest is well developed (Wright and Rausch, 1955). Wright and Rausch (1955) conclude that no one cranial measurement alone is critical in distinguishing adults from immatures. These observations and my data agree that at best cranial and canine dimensions can place an individual in either of two broadly defined age classes, juvenile or adult. The appearance of the skull (length and development of saggital crest, suture closure, etc.) can be deceptive when trying to age wolverine and should not be regarded as an accurate age indicator (Philip Wright, personal communication).

Rausch and Pearson (1972) concluded that for wolverine, only cementum analysis provides a reliable estimate of age beyond one year. They note, however, that consistently readable tooth sections are not produced and annulations are not as distinct as for other animals. Matson (1980) reports that the wolverine canine section is among the most difficult to age.

The cause of formation of annual layers in teeth or bone is the regular seasonal variation in growth rate. Usually this is understood to mean rapid growth in the summer with a slow down in the winter (Morris,1972, Klezeval and Kleinenberg, 1967). The wolverine scavenges in winter and is omnivorous in summer, with winter having the greatest food abundance (Rausch and Pearson, 1972; van Zyll de Jong, 1975; Hornocker and Hash, 1981). It is likely that discontinuities in growth rate are not as pronounced as in other mammals or tend to vary depending on favourable years. Distinct cycles of nutrient intake and growth are believed to explain the success of cementum analysis for aging hibernating mammals (Philip Wright, personal communication). In wolverine, however, cementum deposition would not occur in a regular pattern and may account for difficulties in aging canine sections. Because the enamel line technique is also based on the deposition of cementum, this could explain why a strong correlation with absolute age was not found.

Problems of aging canine sections should be secondary to the fact that the validity of the technique in wolverine has never been shown. It is generally assumed that numbers of annuli correspond to age (Morris, 1972). However, this cannot be verified without knowing the rate of cementum deposition (Morris, 1972). The extent of published evidence in wolverine is from Myhre (1968) who found a good correlation between layers of tooth

cementum and two wolverines of known ages. Magoun was able to correlate number of annuli in canines with age in three known-age wolverines, however, she notes that preparation of teeth is extremely important (Audrey Magoun, personal communication). Hornocker (personal communication) however, obtained no positive results with annuli using a variety of methods, including sectioning the jaw. Wright (personal communication) has done extensive research on aging wolverine. Presently he is using discriminant analysis to analyze the effectiveness of a number of methods, including use of cranial dimensions and cementum analysis, and believes he will be able to supply estimates of accuracy for the various techniques (Philip Wright, personal communication). Most difficulties, he found, arise in the differentiation of juveniles from yearlings, also shown by my lack of discrimination between juveniles and subadults. Wright did not obtain positive results with cementum analysis and concludes the wolverine is not a good candidate for aging by this method in comparison with other mustelids. He has achieved the most promising results by using diameter of the canine pulp cavity in relation to the diameter of the exterior of the tooth. Wright has found that it is simple to distinguish juveniles from yearlings in early fall as diameter of the pulp cavity is very large in the former as compared to the latter. By late winter, however, he notes that the cavity has closed considerably and distinguishing between these two age classes is much more difficult.

Cementum analysis has been used to age wolverine (Matson, 1980, 1981) even though the method has not been verified. The aged series of skulls used in my analyses may not accurately depict age. Dapson (1980) emphasizes that no aging technique should be referenced to another that is unvalidated. It appears that cementum analysis may not be the best method to age wolverine. If using criteria of canine pulp diameter is shown to provide accurate age estimates, this may be the best aging technique for wolverine.

5.4 Discriminant Analyses

5.4.1 Inter-sex Comparisons

Female wolverine are on average slightly smaller than males; measurements are 10% less and weight about 30% less (Hall and Kelson, 1959; Peterson, 1966). Not only did discriminant function analysis allow for classification of unsexed individuals, it also permitted quantification of differences between sexes.

All three regional samples had differing sets of discriminating variables (Tables 7-9). Palatal constriction was the only variable in common for all 3 samples and contributed varying amounts to each function. Negative signs for discriminant coefficients can be interpreted as the effect of a decrease in size. The Mainland female differs from the male in having a narrower skull (smaller post-orbital breadth and ecto-orbital breadth) and a shorter rostrum (shorter maxillary tooth row). The skull of the Mainland male has a broader rostrum and a bigger jaw (increased height of ramus mandibulae). The greatest difference is in rostrum breadth and ecto-orbital breadth, although on the whole differences between all dimensions were not large. Some obvious measurements, such as condylobasal length or length of skull could not be included due to too many missing data. However, selection was from a large group of variables and included the counterparts viscerocranium length and braincase length. High canonical correlations (Tables 7-9) and success of classification (Table 11) for all 3 samples indicate the variables chosen provided good discrimination.

The largest difference between Yukon males and females is in palatal constriction width (Table 8). Braincase height is an important discriminator for Yukon sexes only. Hence, Yukon males are most readily distinguished from females in having a larger skull in 3 dimensions, mastoid breadth, rostrum breadth and braincase height.

The discriminating variable viscerocranium length was unique to the Island inter-sex comparison (Table 9). Only 2 other dimensions were necessary for discrimination, mastoid breadth and palatal constriction. The former provides the greatest discrimination with viscerocranium length providing the least. Island males differ from females most noticeably in having a wider skull, longer rostrum, and wider palatal constriction.

One can quickly gain an appreciation of the relative amount of separation between groups by an examination of the group centroids (Table 10). Four and five tenths, 57.3 and 48.6 units separated males and females in the Mainland, Yukon, and Island populations, respectively. This would indicate that separation between Yukon and Island sexes is more clear than for Mainland sexes. This is also shown in the amount of overlap in the frequency histograms (Figures 5-7) and classification results (Table 11). Overlap occurs only for the Mainland sample where 7 of 49 (14.3%) of individuals were misclassified.

All 3 regional samples used to derive the functions contained juveniles, subadults and adults. More Mainland males (6 of 30) than females (1 of 19) were misclassified. One discriminating variable, ecto-orbital breadth, was also found to distinguish between male adults and juveniles in my age class correlations. Examination of misclassified individuals reveals that on the basis of ecto-orbital breadth, 3 of 6 are juveniles. Between sex overlap can then be partly explained by similarity in certain cranial dimensions between juvenile males and adult females. It should be noted that sample size used to derive the Mainland function is greater than for the other regions. This and the large area the Mainland sample originated from help explain the increased variability.

Varying number of discriminating variables and varying importance indicates that inter-sex differences are not consistent between regions. Flook and Rimmer (1964) established criteria to identify sex from skull fragments using diameter of the upper canine and/or length of the skull, alone or with the dimensions of maxillary toothrow length, mandibular toothrow and lower canine diameter. Of all these, only maxillary toothrow length was identified as a discriminating variable in my analyses and then only for the Mainland sample. Flook and Rimmer's (1964) specimens came from Alberta. Hence, it appears likely that one cannot generalize inter-sex differences in cranial measurements of wolverine from one population or region to the whole species.

5.4.2 Inter-regional Comparisons

The female set of discriminating variables was identical to that of the males but also included ecto-orbital breadth and the height of ramus mandibulae. Hence, distinguishing between females of different groups involves more measurements than needed to distinguish between males.

On the whole, females exhibit less variability. This is readily evident from scatterplots for males (Figure 8) and females (Figure 9). Discrimination among the three populations was not as clear as in discrimination of sex. More variables were involved, each contributing relatively less to the discriminant function. Separation of centroids was also not as great (Tables 13 and 16).

5.4.2.1 Males

For males the largest contribution to discriminant function I was provided by diameter of the upper canine and rostrum breadth (Table 12). Variables contributing the most to function II were upper canine diameter, inter-orbital breadth, lower canine diameter and palatal constriction. Lower canine diameter makes the largest contribution to both discriminant functions . Postorbital breadth appears to contribute little to both functions but was shown to be important as elimination resulted in less efficient discrimination. Function I can be regarded as most important as it explains 72.09% of variability with function II accounting for 27.91%.

Centroid separation in discriminant function I was 4.7, 2.6, and 2.2 units for Mainland:Yukon, Mainland:Island, and Yukon:Island pairs, respectively (from Table 13). Separation distances in function II were 1.7, 2.6, and 2.2 for the same group pairs. Separation of males in the three populations is not large with Yukon and Island males being the most alike and Yukon and Mainland males the most dissimilar.

Discriminant function I can be considered as a Mainland-Yukon axis, in regards to the most different groups. In decreasing importance, Mainland and Yukon males differ most in dimensions of diameter of upper canine, rostrum breadth, interorbital breadth, diameter of lower canine, viscerocranium length and zygomatic breadth (Table 12). Function II explains further separation of Yukon and Island males from Mainland males. In descending order, these are most dissimilar regarding diameter of upper canine, interorbital breadth, viscerocranium length, diameter of lower canine, and palatal constriction. Differences from function II are of a lesser magnitude than those arising from function I.

Overlap occurs between Island and both Yukon and Mainland males (Figure 8). Both Mainland and Yukon groups exhibited considerable variation while Island males displayed very little.

Sample sizes consisted of 14 Mainland, 2 Yukon and 4 Island individuals. Insufficient sample size may explain the excess and lack of variation in the Yukon and Island groups, respectively. The three pairs of regions differ in regards to the variables that discriminate between them. A high percentage of Mainland (32 of 34) and Island (4 of 4) males were correctly classified (Table 14). 3 of 7 Yukon males were correctly classified, 3 were misclassified as Mainland and 1 as Yukon.

I was able to obtain greater correct classification of Yukon males by altering the set of discriminating variables and thus increasing sample size. However, correct classification of both Mainland and Island males concomitantly decreased. Since Mainland sample size was altered little by this action, it can be concluded that the variables themselves as well as decreased sample size, for the Island sample, were the causes of misclassification. This would indicate that cranial measurements that are different for two regions may not be the same dimensions that differ most noticeably when compared with other regions. The allocation of individuals in the classification stage reveals that Yukon males could not be differentiated from Mainland males, regarding the variables considered, while fewer Mainland (0 of 34) and Yukon (1 of 7) were assigned to Island origin (Table 14).

Mainland specimens originated from a far larger area than either Yukon or Island males (Figures 1 and 2). The scatterplot (Fig. 8) reveals the extent of variability within the regions. It appears that Mainland males could be divided into at least three groups. This would suggest the possibility of regional populations occurring on the Mainland.

5.4.2.2 Females

For females rostrum breadth contributes most to function I followed by diameter of lower canine and postorbital breadth (Table 15). Ecto-orbital breadth and interorbital breadth were the largest contributors to function II. Function I can be considered the most important as it accounts for 88.35% of the variability.

Centroid differences for function I are 5.2, 4.3 and 2.1 units for Mainland:Yukon, Yukon:Island and Island:Mainland group pairs, respectively (from Table 16). Function I is primarly a Mainland-Yukon axis and secondarily a Yukon-Island axis in regards to the greatest divergence between regions.

Centroid differences for function II are 2.4, 2.2 and 0.2 units for Yukon:Island, Mainland:Island and Mainland:Yukon pairs. Function II accounts for differences between the Island and other two regions although these are of a lesser importance to the discrimination (11.65%).

Females of all three groups exhibit considerably less variability than do males (Fig. 9). The greatest variation occurs within Mainland females, however, as for males, this may not be evident in the other two groups due to the smaller sample sizes (5 Yukon, 3 Island). 1 of 7 Yukon females was misclassified as Island and 6 of 7 correctly as Yukon (Table 17). As seen from the scatterplot, (Fig. 9), the misclassified individual could have easily been included in the Yukon sample. Location of groups in space indicates a greater similarity between the Island and other regions than between Yukon and Mainland regions.

Mainland females were misclassified 2 of 24 times as Island and 1 of 24 as Yukon. As for males, the location of these individuals indicates the possibility that the Mainland sample may be composed of at least three regional populations (Fig. 11). Considering the large area involved and the ability of the discriminant analyses to distinguish between specimens from geographically adjacent regions, this is not unlikely. A larger sample size is necessary in order to identify the extent of variation within different areas of the Mainland. However, considering that all three samples were taken from throughout their respective regions, the results obtained are likely to be good estimates of the actual variability within the different populations.

5.4.3 Summary and Interpretations

High classification results indicated unknown individuals could be sexed with little error. In general males are larger than females in cranial dimensions. Inter-sex differences for Island and Yukon regions are greater than for Mainland sexes. Zimmerman and Ludwig (1974), using a moderate number of characters and small sample sizes, obtained results which permitted discrimination to a fine degree among apparently very similar populations of aquatic beetles (Rhantus gutticollis). Hence, the technique may be used as an indication of the minimum number of measurements and sample size necessary for discrimination. High degree of separation between males and females indicated Island and Yukon sample sizes were adequate for

sex discrimination. Overlap for Mainland sexes may have been due to the confounding effect of age. Significant D^2 values indicate that the variables chosen accurately depicted inter-sex differences. At most, only 6 dimensions were necessary for sex discrimination. Skulls from the three regions differ in the cranial dimensions that distinguish between sexes, hence differences in sexes from one population or region cannot be applied to the entire species.

Discrimination of regions is not as clear as for sexes, differences being of a lesser magnitude. Ten to 12 variables were required, each making relatively smaller contributions. Cranial dimensions that discriminate between 2 regions are not the same for all regions. Hence, a general statement regarding differences in skull size cannot be made. Females from the 3 regions are similar in more dimensions than are males. Mainland and Yukon regions differ most for both males and females while Island and Mainland females, and Island and Yukon males are most similar. Efficiency of discrimination was limited by sample size of Island skulls. Additional specimens would reduce variability of results.

Sample sizes were deemed sufficient for all except Yukon males, which was more likely an effect of inefficient discriminators rather than insufficient sample size. Both Mainland sexes exhibit great variability. It appears the Mainland sample may be composed of more than one regional population. Considering the area of distribution, this is not unlikely. Island males and females, and Yukon females exhibited little variability. As specimens were obtained from throughout their respective regions, it is likely that my results accurately depict true variation between populations.

Goldman (1935) described the type specimen of G. g. vancouverensis as very similar to Mainland wolverine although differing by having broader zygomata, a narrower palate, smaller auditory bullae, greater developed palatopterygoids, shorter mandible length and rather heavy dentition. Cowan (1936) noted that Island wolverine differ in having the skull relatively narrower in all parts except the width of the "frontal shield", and in having slightly heavier teeth. He did not find the other differences described by Goldman (1935) but noted that the foramen magnum is more rounded and less flattened dorso-ventrally (Cowan, 1936).

Diameter of both upper and lower canines were important in discriminating among the three regions in my analyses, with zygomatic breadth and palatal constriction being lesser

contributors. Mandible length was not found to be a contributing variable, and I could not discern the other differences mentioned by Goldman (1935) in the eight skulls I examined. A t-test indicated a significant difference ($P \leq .013$) in foramen magnum width and length between Mainland and Island pooled samples and in foramen magnum width between Island and Yukon pooled samples ($P \leq .017$) (Appendix 4). However, because of missing data I was unable to include these variables in the discrimination analyses. There was an indication that foramen magnum length could distinguish between juveniles and adults, hence age may have been a confounding effect for Goldman (1935). If a larger Vancouver Island sample becomes available, this difference should be examined.

Inter-regional differences can be interpreted in terms of population genetics or as the effect of modifying environmental factors. Huson and Page (1979) suggest differences in cranial measurements in regional populations of red fox likely reflect differences in environment in terms of diet, available habitat and climate. Colour and size difference in wolverine have been accounted for by individual variation. Geographical variability is reported as slight although it has not been adequately studied.

Environmental conditions vary throughout the extensive range of Gulo gulo. Such environmental differences may induce gradual phenotypical variation directly as well as genotypical variation indirectly (Jolicoeur, 1959). The effect of insular isolation on genotype has been discussed. Direct effects of environment on physiological processes and morphological characteristics in vertebrates have been demonstrated. Bissonnette and Bailey (1944) controlled molts and coat colour changes in weasels photoperiodically. Jolicoeur (1959) attributes geographical variation in the wolf to seasonal periodicity. He concludes that the circumstances in which local populations live might induce modifications of growth processes, including those involved in skull development (Jolicoeur, 1959).

Regarding the status of Vancouver Island wolverine, the most important systematic problem is the extent to which biometrical characteristics are genotypical or phenotypical. Geographical variation can be used as a basis for taxonomic decisions only if it is hereditary. Variation among skulls from the three regions studied is slight and the amount that can be attributed to heredity is unknown. More material from Yukon, Arctic regions, British Columbia and Alberta is required to delimit the extent of regional differentiation. It is difficult to establish population

characteristics for wolverine (ie., residence, transience, dispersion) (Hornocker and Hash, 1981), hence effects of gene flow are not easily determined. Until such information becomes available from extensive field studies, results from biometrical comparisons must be interpreted with caution.

5.5 Management of wolverine in British Columbia

van Zyll de Jong (1975) cites human predation and settlement as reasons for decline of wolverine in eastern Canada. Comparatively stable and denser populations in mountainous areas (British Columbia and the Yukon) or more remote areas (Northwest Terrritories) are explained by the availability of natural refuges created by relative inaccessibility and low density of human predators (van Zyll de Jong, 1975).

Krott (1959) cites low density and smaller litter size (2-5) as reasons for the wolverine's reduced ability to compensate for losses due to human predation. van Zyll de Jong (1975) suggests that the scavenger role of wolverine implies a direct relationship between biomass and turnover of large herbivore populations and abundance and distribution of wolverine. This is supported by evidence of concomitant declines of wolverine and caribou populations in Labrador (Banfield and Tener, 1958; van Zyll de Jong, 1975). Hornocker and Hash (1981) note that availability of carrion depends to a large extent on the status and condition of large ungulate populations inhabiting an area. A greater wolverine density in Montana is suggested as a result of a more plentiful food supply in the form of large and diverse ungulate populations (Hornocker and Hash, 1981).

One of the objectives of the Fish and Wildlife Branch (1979) is to protect critical habitats for mustelids, primarily mature conifer stands for wolverine. Wolverine are noted to prefer taiga or talus slopes and are adversely affected by large scale clear cut logging (Fish and Wildlife Branch, 1979). Osmond-Jones et al. (1977) report that wolverine in Tatlatui Park are usually found in alpine areas and along talus slopes as well as in lower areas. Penner (1976), in a winter track study in Alberta, found 100% utilization of undisturbed areas (75.1% of the study area), compared with large cleared areas, roads and recent or old cut line. The majority of wolverine tracks observed were in areas subjected to relatively minor disturbance (Penner, 1976). Due to low sample sizes, no statistical comparisons with environmental

parameters were conducted (Penner, 1976). In Montana, wolverine appeared to select Abies cover types throughout the year (Hornocker and Hash, 1981). Large areas of medium or scattered mature timber accounted for 70% of habitat use; areas of dense young timber were used least (Hornocker and Hash, 1981). Cover provided by mature or intermediate timber was shown to be important in habitat selection (Hornocker and Hash, 1981). Food, in the form of carrion and small mammals, was apparently more available in these habitats, especially in edge and ecotonal areas around cliffs, slides, blowdowns, basins, swamps and meadows (Hornocker and Hash, 1981). These areas were also prefered by fisher (Martes pennanti) and marten (Martes martes) (Hornocker and Hash, 1981). Habitat requirements for wolverine in British Columbia have not been established. Need for this information has been noted by the Fish and Wildlife Branch (1979) and Holbrow (1976). Holbrow (1976) also recommends that specific data is required on methods of determining density, population structure and feeding habits. Due to inaccessibility of habitat and extensive ranges of wolverine, population characteristics are difficult to establish (Hornocker and Hash, 1981).

From his observations and interviews with trappers, biologists and government officials, Holbrow (1976) agrees that the status of wolverine does not appear to be endangered in Western Canada. He makes the following recommendations for British Columbia; wolverine should be removed from game status (in some areas wolverine may be taken by licenced hunters), or failing that, the prohibition of hunting in certain areas (Holbrow, 1976). Completely closed seasons for the southern portion of Vancouver Island, the islands in the Strait of Georgia and the Okanagan and Similkameen districts is also recommended (Holbrow, 1976). There is no open season for wolverine on Vancouver Island.

5.6 Conclusions

Distribution of wolverine in British Columbia is widespread. The species appears fairly abundant in the provincial parks (excluding the south-western areas) and regions surrounding Prince George, Dawson Creek, Mackenzie, Germanson Landing, Pink Mountain, Fort Nelson and northern areas of the province. It is rarely sighted in coastal areas. Distribution has changed little in British Columbia since the turn of the century. Human settlement and predation are cited as reasons for decline in

eastern Canada. Abundance of wolverine has been relatively stable in British Columbia due to the presence of remote and inaccessible areas. It is recommended that critical habitat requirements be determined for wolverine in British Columbia and appropriate management action taken to ensure its secure status in the province. Gulo gulo vancouverensis is found mainly on the central mountain ranges of Vancouver Island. The subspecies is rarely sighted or trapped and a population estimate cannot be provided.

Age determination in wolverine is difficult. Most problems arise in distinguishing juveniles from subadults (yearlings). Criteria using diameter of the canine pulp cavity may be useful in this respect. Age of wolverine cannot be accurately estimated from skull appearance. At best, certain cranial dimensions can discriminate between juveniles and adults. Wolverine are not good candidates for aging by cementum analysis. The enamel line technique is not recommended for aging wolverine and it is doubtful whether field aging techniques will prove useful in this species.

Multiple discriminant analysis has great potential as a basis for examining population differentiation and its causes (Zimmerman and Lugwig, 1974). Only a moderate number of parameters and a small sample size may be necessary to provide good discrimination. Differences occur in populations from Yukon, British Columbia mainland and Vancouver Island regions. It is likely that more than one regional population occurs on the Mainland. More information is necessary on cranial variation of wolverine within British Columbia.

Considering the similarity of wolverine throughout its entire range, it is likely inter-regional differences noted are due to environmental modifications. It is difficult to establish population estimates and characteristics for wolverine. No field studies are available for British Columbia, hence factors behind regional differences cannot be determined at the present time. Information on population dynamics of wolverine in the province is necessary.

Vancouver Island wolverine differ from those on the Mainland in certain cranial dimensions. These differences are not of a greater magnitude and perhaps less than those between Mainland and Yukon regions. Colour differences are not a sound basis for subspecific classification and could not be wholly substantiated for Mainland and Vancouver Island wolverine (Appendix 5). More information is necessary on colour variation in wolverine within

the British Columbia mainland.

On the basis of my results, subspecific designation for Gulo gulo vancouverensis is not warranted. However, the rarity of wolverine on Vancouver Island merits their protection. As regional differences in cranial dimensions and possibly in external characteristics are apparent and may be considered a product of habitat and environment, it may be useful to retain the classification of subspecies for management purposes.

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1 Listing of Mainland and Yukon specimens

Mainland				Yukon
UBC	141	BCPM	W46K	HJ-78-13
UBC	149	BCPM	69090277	HJ-78-14
UBC	179	BCPM	729251277	HJ-78-20
UBC	875	BCPM	W31K	HJ-79-1
UBC	3486	BCPM	625020277	HJ-79-277
UBC	3935	BCPM	748060277	HJ-79-302
UBC	4141	BCPM	W5K	HJ-79-356
UBC	6189	BCPM	W30K	HJ-79-361
UBC	6190	BCPM	52191276	HJ-79-362
UBC	7628	BCPM	W29K	HJ-79-362A
UBC	8056	BCPM	729280277	GG-79-1
UBC	9468	BCPM	W19K	GG-79-3
BCPM	1341	BCPM	W3K	GG-79-4
BCPM	1342	BCPM	616050377	UBC 7343
BCPM	1411	BCPM	W56K	
BCPM	1412	BCPM	W1K	
BCPM	5820	BCPM	W55K	
BCPM	6823	BCPM	729100177	
BCPM	9276	BCPM	728221176	
BCPM	9994	BCPM	726152276	
BCPM	10282	BCPM	343160177	
BCPM	10283	BCPM	65310177	
BCPM	10284	BCPM	729270277	
BCPM	10285	BCPM	Barry Clan	
BCPM	10286	BCPM	W18K	
BCPM	10287	BCPM	73020277	
BCPM	W3K	BCPM	W22K	
BCPM	721140277	BCPM	68070177	
BCPM	617B020177	BCPM	unknown	

2 Trapping locations of British Columbia Mainland specimens held by the BCPM and UBC according to management unit

2. Lower Mainland		3. Thompson-Okanagan	
Alfred Mt.		Cottonwood Cr.	
Phillips Arm	2	N. Thompson R.	2
		Rutland	
	3(3%)		4(4%)

4. Kootenay		5. Cariboo	
Bernard Cr.	2	Quesnel R.	
Mt. Revelstoke	2	Horsefly R.	
Nelson		Blackwater R.	5
St. Mary's Lake		Redwater L.	
		Snowshoe Cr.	
	6(7%)	Bella Coola	3
		Bell Mt.	
			13(15%)

6. Skeena			
Clemretta		Mclaske L.	
Mt. Colley	2	Blue R.	2
Burns Lake		Johnny L.	
Ootsa Lake		(unknown)	
Francoise Lake	2		
Tahtsa Lake			26(30%)
Hazelton	2		
Kispiox Valley			
Burdick Cr.			
O'Donnell R.			
Atlin			
Driftwood Cr.			
Stewart			
Snowbank Cr.			
Collins L.			
Telkwa			
Smithers			
Denise L.			

7. Omineca - Peace

Wansa L.	
Redwillow R.	
Bijioux Falls	2
McKale R.	
Swiftcurrent R.	
Holmes R.	2
Small Cr.	
Croyden	2
Canoe R.	
Castle R.	
Dore R.	2
Dunster	
Engen	
Eulatazella L.	
Ospika R.	4
Wicked R.	
Milk R.	2
Chicken Cr.	
Manson R.	
Buckinghorse R.	2
Trapper Cr.	
Blue L.	
East Pine R.	2
Mt. Robson	
	36(41%)
TOTAL	88(100%)

3 Trapping and sighting locations for Vancouver Island wolverine

Trappings

Date	Location	(no.)	Source
1891	unknown		BCPM 1343
1900's	Central L.		Bud Frost, Port Alberni
1907	Cowichan L.		BCPM 1570
1910	Klanawa R.	(2)	BCPM records
1910-11	Nootka Sound		Swarth, 1912
1912	near Alberni		Swarth, 1912
1912	Friendly Cove	(1-2/y)	Swarth, 1912
1913	Central L.		USNM 211499
1920's	Coleman Cr.		Bud Frost, Port Alberni
1920's	Union Bay		Skate Hames, Campbell River
1930's	Camp Bay		BCPM records
1932	Jump Cr.		Fish and Wildlife, Nanaimo
1937	Cameron R.		BCPM 2486
1946	Tsable R.		UBC 1745
1949	Cameron R.		UBC 3510
1952	Claud Elliott L.		Port Alberni museum
1978	Rooney L.		BCPM 9872
U	Zeballos		Cowan and Guiguet, 1965
U	Fanny Bay		Cowan and Guiguet, 1965
U	Jordan Meadows		Cowan and Guiguet, 1965
U	Shawnigan L.		Cowan and Guiguet, 1965

Sightings

Date	Location	(no.) (T=tracks)	Source
U	Brooks Peninsula		Dan Workman, Conservation officer, Port Hardy
1930's	Oyster R.	(T)	Skate Hames, Campbell River
1940's	Constitution Hill	(den)	Skate Hames, Campbell River
1961	Flores Is.	(T)	BCPM records
1965	Marshall L. (Northwest Bay)		Byron Mason, Fish and Wildlife, Nanaimo
1968-69	Nimpkish R.	(5)	Bud Frost, Port Alberni
1973-74	Nimpkish Valley		Frank Wilson, Nanaimo
1975	Mt. Joan	(3)	Fish and Wildlife, Nanaimo
1975	Herbert Inlet	(T)	Pat Browne-Clayton, Conservation officer, Campbell River
1977	O'Connell L. (Mahatta River)		Byron Mason, Fish and Wildlife, Nanaimo
1978	Nanaimo Lks.		BCPM records
1979	L. Cowichan		Fish and Wildlife, Nanaimo
1981	L. Cowichan		Fish and Wildlife, Nanaimo

4 One-tailed t-test to examine differences in FML and FMW between region pairs for pooled samples

Comparison	Results
Mainland:Yukon (38:11)	not significant
Mainland:Island (38:4)	FML(Island) > FML(Mainland) P=0.013 FMW(Island) > FMW(Mainland) P=0.011
Yukon:Island (11:4)	FML(Island) > FML(Yukon) P=0.120 FMW(Island) > FMW(Yukon) P=0.017

5 Colouration of Pelage

General colour in wolverine is dark brown with pale lateral stripes running from shoulder to rump and merging posteriorly to extend down the proximal half of the tail (Cowan and Guiguet, 1965). Underparts are dark, often with irregular white or orange throat markings (Cowan and Guiguet, 1965). Colour scheme varies considerably from totally pale brown or buff (almost albino, Jackson, 1961) to glossy brown with no lateral stripes (Holbrow, 1976). Holbrow (1976) presents two photos, one depicting typical colouration and the other an almost albino animal ("rare") with dark legs and orange near the underparts close to the rear legs.

Colour variation throughout the circumpolar range of Gulo gulo is extensive, and not confined to either North America or Eurasia (Audubon and Bachman, 1854). Audubon and Bachman (1854) describe American specimens from polar regions that were as "fully black" as those from Russia. Anderson (1926) reports that colour can vary from almost black with purple to light yellow and buffy. He concluded that wolverine races based on fur colour are untenable (Anderson, 1926).

Elliot (1903, 1905a and b), Goldman (1935), Dagg and Campbell (1974) and others remark that geographic differences may account for variations in pelt quality, size and colour. Seton (1926) described "typical" colouration in a Hudson Bay wolverine, a "generally pale" specimen from California and a very dark wolverine with no buff from Alaska. However, Novikov (1956) states that while individual variation is extensive in Gulo, geographic variation is slight and has not been adequately studied.

Some differences due to sex and age have been reported. Seton (1926) notes that paler specimens are usually female. This has not been reported by others. Ross (1835) writes that younger wolverine are darker and that older animals have more gray markings. Lighter colouration in younger wolverine was also observed by Holbrow (1976). Green (1956) noted no seasonal variation in colour.

Reports on pelage colouration of G. g. vancouverensis differ. Hall (1932) found no differences between an Island pelt and a Mainland pelt. Swarth (1912) described an animal killed near Nootka Sound as "extremely dark coloured" compared with wolverine from Alaska. Anderson (1946) describes the species as a "dark, insular race". A sighting from Cowichan Lake described the

species as much darker than on the Mainland (Fish and Wildlife Branch, Nanaimo, personal communication). Cowan and Guiguet (1965) describe the subspecies as darker. Cowan (1936) describes one specimen as lighter in colour throughout. However, he notes that "colours of wolverine are so variable that without corrobative evidence it is not safe to assume differences to be racially diagnostic".

I examined 4 Mainland pelts and 3 from Vancouver Island. All Mainland pelts exhibited "typical colouration" as described by Cowan and Guiguet (1965), with differences in colour intensity and presence or absence of markings.

Pelage colour in both G. gulo and G. g. vancouverensis is variable. Differences, if any, between Island and Mainland pelts cann. be precisely defined from specimens available. However, all of the sightings I obtained described the animal as very dark or black with light markings (Ken Hallberg, Ralph Wilson, Skate Hames, Fish and Wildlife, Nanaimo; personal communications). More information is necessary in order to determine the amount of colour variability in Gulo throughout British Columbia.

Size differences should also be mentioned. Cowan and Guiguet (1965) describe the subspecies as a smaller race. Available specimens do not represent an adequate sample and a definite conclusion regarding size differences is not possible.